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The coupling of biogeochemical cycles of nutrients

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Abstract. For any element which is incorporated into biomass, the biogeochemical cycle of that element in a given ecosystem will be coupled to that of any other element similarly incorporated. The mutual interaction of two such cycles is examined using a simple model in which each cycle is constrained into four compartments. In each cycle the assimilation rate (primary productivity) is related in a non-linear fashion to the two nutrients and to biomass. The interactions are represented by combining a hyperbolic dependence for each nutrient (involving a "Michaelis constant") with a logistic equation governing the dependence of rate on biomass (involving a "carrying capacity"). The response of the model to perturbation (e.g. mobilization of an abiotic reserve) is strongly governed by the values assigned to these constants. The coupled cycles can exhibit positive feed-back with anomalous responses of the steady state and time-dependent solutions may exhibit complex oscillatory behaviour. Both the steady-state sensitivity and the kinetic behaviour of such coupled systems are simplified if the range of atomic ratios permitted by the assimilation process is restricted. It will therefore be of importance to determine under what conditions the assimilation rates for different elements are governed by mass-action effects (Liebig's Law) or by stoichiometric constraints (Redfield ratios).

Introduction

One of the major outstanding general problems of global biogeochemistry concerns the interactions of the cycles of individual elements. Likens [1981] states: "It has become increasingly apparent that a realistic understanding of individual cycles is not possible in isolation from other interacting cycles, and although integrative analyses are awesome it is clear that attempts must be made to take a more holistic approach to global biogeochemistry." In the same volume, from the preface to which that quotation is taken, there are a number of chapters on interactions between cycles. In one of these [Likens, Bormann and Johnson, 1981] the authors, writing of anthropogenic perturbation by combustion of fossil fuels, application of agricultural fertilizers and pesticides, deforestation, erosion and irrigation, state: "There is almost no useful quantitative information on interaction between global cycles, but we suspect that interactive effects may outweigh individual effects that we know for single systems".

The purpose of this paper is to indicate a number of theoretical questions which must be answered in any study of interacting biogeochemical cycles and, in particular, to point to a dilemma which has not, to the best of my knowledge,

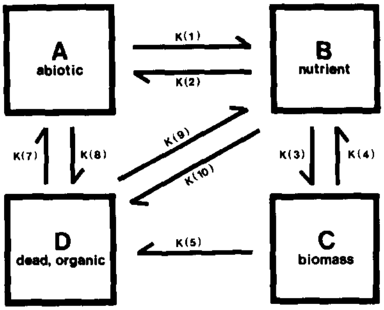

Figure 1. A four-box model of ecosystem structure.

received any formal consideration. If it is assumed that biogeochemical cycles are coupled through the incorporation of nutrient elements into biomass, then the crucial question becomes: are the relative rates of incorporation of the elements governed by the law of mass-action (Liebigs's Law) or by the stoichiometric composition of biomass (Redfield's ratios)? It is not clear that currently available data can answer this question. One can however use data available in the literature to construct simple ecosystem models and demonstrate that both the steady-state and time-dependent behaviour of such models differ very markedly according to the answer which is assumed to this question.

The strategy of this paper is to represent the cycling of a given nutrient element within a highly simplified ecosystem model consisting of only four compartments. The interaction of an isomorphous cycle of a second element is then treated as a mutual perturbation of nutrient incorporation into biomass.

A four-box ecosystem model

The generalized model is depicted in Fig. 1. Similar models are not uncommon in the literature of ecology [Bormann and Likens, 1979], geochemistry [Lasaga, 1980] and oceanography [Garrels and Perry, 1974]. Such models are not simula-

Table 1. Rate equations for the four box model

$$dA/dt = -(K(1) + K(8))\cdot A + K(2)\cdot B + K(7)\cdot D$$

$$dB/dt = -R(bc) - (K(2) + K(10))\cdot B + K(1)\cdot A + K(4)\cdot C + K(9)\cdot D$$

$$dC/dt = R(bc) - (K(4) + K(5))\cdot C$$

$$dD/dt = -(K(7) + K(9))\cdot D + K(5)\cdot C + K(8)\cdot A + K(10)\cdot B$$

for R(bc) see Equation (1) in the text

The corresponding rate-constants for the second cycle of Figure 3 and Table III use suffixes from 11 to 20, e.g.,

$$dX/dt = -R(xy) - (K(12) + K(20))\cdot X + K(11)\cdot W + K(14)\cdot Y + K(19)\cdot Z$$

tions of reality but function rather as heuristic devices useful for generating questions about ecosystems in nature. Their function is not representation but to aid in formulating hypotheses. Apart from a few papers such as that by Lasaga [1980] and, particularly, the pioneering analysis of Eriksson and Welander [1956] little attention has been given to working out the formal kinetic relationships of such models. The rate equations for the model are given in Table 1. In common with most simple models it is assumed that all but one of the rates are linear, donor-controlled, e.g. the rate of flow from the abiotic pool A to the nutrient compartment B, $R(ab) = K(1)\cdot A$. The only exception to this statement is R(bc), the rate of flow from B to the biota, C. This flow which may be equated to the assimilation rate, [Eriksson and Welander, 1956] or gross primary productivity of the ecosystem [Whittaker and Marks, 1975] for the element under consideration, requires some detailed attention because it turns out that the dynamics of the model as a whole are strongly influenced by the way in which this rate is determined.

The dependence of growth on a limiting nutrient was clearly formulated by Liebig at the conclusion of his paper [Liebig, 1855], ". . . the growth and the development of a plant depend on the assimilation of certain bodies, which act by virtue of their mass or substances. This action is within certain limits directly proportional to the mass or quantity of these substances . . .". Liebig's qualitative statement is given algebraic expression in the formulation of Monod (1942) for microbial growth, i.e. the rate dependence on B is similar to that given by the Michaelis-Menten equation, i.e. $R(bc) \propto B/(M + B)$. The rate is therefore somewhere between zero-order and first-order in B depending upon the value of M. In other approaches this fractional-order dependence is defined, e.g. by the biota growth factor of Bacastow and Keeling [1973].

It is common to write this rate, R(bc), as also being linear in C when the rate is said to be recipient-controlled [Harwell et al., 1981] or autocatalytic [Lasaga 1980] i.e. $R(bc) \propto C$. This is however an unsatisfactory approach as it permits indefinite exponential growth of the biota. It turns out to be useful to incorporate a limiting upper level for C as in the density-dependent equation for population growth, an approach which has been suggested also by R.B.Williams [1972] who refers to it as "controlled non-linear transfer". These consideration yield equation

$$R(bc) = \frac{K(3)\cdot B\cdot C}{M + B}\cdot\frac{C(m) - C}{C(m)} \tag{1}$$

where M is the "Michaelis-constant" for the dependence of gross primary productivity on the nutrient under consideration and C(m) is a maximum size for the biota pool expressed in moles of the same nutrient. All quantities and fluxes are expressed in molar terms in order to make possible comparison of flows of different elements. Of course, for high values of M and C(m) this equation reduces to the second-order equation more commonly used. The use of M and C(m) allows one to vary the relationship between assimilation rate, nutrient concentration and biomass. Eriksson and Welander [1958] were the

Table 2. Standard values for a global carbon cycle

10^{15} moles or 10^{15} moles$\cdot$y^{-1}		Definition	Reference
A	4000	deep ocean C(inorg) + sediment available for dissolution + fossil fuel	Bolin et al. 1979, Table 1.1
B	200	atmosphere + surface ocean C(inorg)	Bolin et al. 1979, Table 1.1 Siegenthaler and Oeschger 1978, "ocean 2B"
C	60	terrestrial biota	Bolin et al. 1979, Table 1.1
D	300	ocean C(org) + soil humus	Bolin et al. 1979, Table 1.1
R(ab)	3	intermediate → surface water	Bolin et al. 1979, Fig.1.18
R(ba)	2.7	R(ab) − R(da)	
R(bc)	11	gross primary productivity = net terrestrial primary productivity*1.75 + oceanic primary productivity	Lieth 1975, Table 10.1 Bolin et al. 1979, Table 1.1
R(cb)	6	R(bc) − R(cd)	
R(cd)	5	net terrestrial primary productivity + R(da)	
R(da)	0.3	decomposition of deep ocean C(org)	Stuiver 1973 p.17 Bjorkstrom 1979 p.440
R(db)	4.7	R(cd) − R(da)	

first to emphasize that the behaviour of the system as a whole is critically dependent on this relationship. In this paper whenever it is desired to demonstrate the effects of changing M or C(m), K(3) is always adjusted to ensure that the standard steady-state solution (from Tables 2 and 3) is retained, i.e.

$$\mathrm{K(3)} = \frac{\mathrm{R(bc\ std)}}{\mathrm{C(std)}} \cdot \frac{(\mathrm{M} + \mathrm{B(std)})}{\mathrm{B(std)}} \cdot \frac{\mathrm{C(m)}}{(\mathrm{C(m)} - \mathrm{C(std)})} \qquad (2)$$

It is for this reason that families of curves such as those of Figs. 2, 5 and 6 all pass through a common point corresponding to the standard compartmental size at the standard value of the rate-constant which is being perturbed:

In the subsequent discussion of the interaction of two models of nutrient cycles, the impact of a second nutrient on the process of assimilation will be treated as equivalent to a perturbation in the rate-constant governing that process (i.e. K(3)). It is therefore necessary to demonstrate the sensitivity of the steady-state of the model to such perturbation. For this demonstration the numerical values used are taken from a simplified version of the global carbon cycle. The standard values for box sizes and intercompartmental flow rates are given in Table 2. Note that in this version both K(8) and K(10) are set equal to zero. A graphic presentation of a sensitivity analysis carried out on this system is shown in Fig.2. The slopes of the curves at the vertical line (indicating the standard value of K(3)) measure the sensitivity of the steady-state to changes in the rate constant for CO_2 fixation into the biota (gross primary productivity).

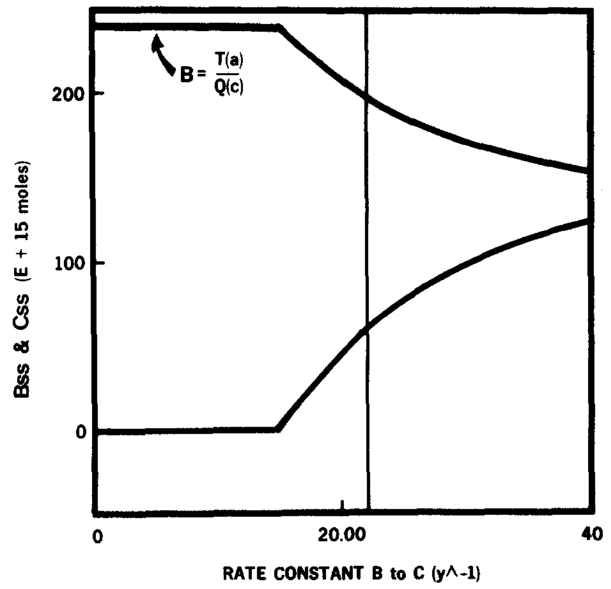

Figure 2. Steady-state values of the nutrient pool (B) (upper curve) and the biota (C) (lower curve) in a global carbon cycle as a function of K(3). The values on the abscissa are given for K(3)·C(std)·(C(m) − C(std))/C(m). The standard value of K(3) indicated by the vertical line is calculated according to equation 2 using C(m) = 240 and M = 200.T(a) = A + B + C + D; Q(c) = 1 + K(2)/K(1). Other values are documented in Table 2.

Interaction of two nutrient cycles. Liebig's law

Figure 2 is illustrative of the way in which the steady-state of a four-box system might be affected by a change in the rate-constant characterizing gross primary productivity. Such a change might occur in response to a variety of environmental alterations e.g. seasonal increase and decrease of illumination. Another obvious way of affecting K(3) is by an alteration in the supply of some second nutrient e.g. if box B represents CO_2, then the rate of fixation of carbon might be influenced by the availability of nitrogen. Ecologists have tended to avoid the question of the dependence of growth on more than one limiting nutrient by invoking the ecological generalisation known as Liebig's "law of the minimum". The relevant formulation of this law is that given by Liebig [1855] in Proposition 40, "The absence or deficiency, or the want of available form, in that one constituent, renders the others which are present ineffectual, or diminishes their efficacy." and Proposition 41, " By the deficiency or absence of one necessary constituent, all the others being present, the soil is rendered barren for all those crops to the life of which that one constituent is indispensable." It is not however necessary to adopt this position and, if one considers the four-box model of Fig. 1, a second nutrient may be represented by X and one can make K(3) and/or C(m) dependent on X; in this paper it is assumed that both the growth rate-constant and the carrying capacity are similarly affected. It is logical

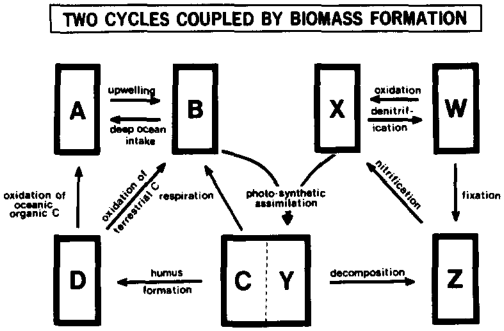

Figure 3. A two coupled four-box model for nutrient interaction with processes specified as in Tables 2 and 3.

to suppose that, if the rate of growth is dependent upon the nutrient pool, B, in a manner which leads to saturation, then the dependence upon the second nutrient, X, should also be written as a Michaelis-Menten type relationship. These considerations lead to equation 3:

$$R(bc) = \frac{K(3) \cdot B \cdot C}{M + B} \cdot \frac{C(m) \cdot (X/(Nn + X)) - C}{C(m)} \tag{3}$$

where Nn is the "Michaelis-constant" for the dependence of K(3) and C(m) upon the second nutrient X. If it is now supposed that X is itself a component of an isomorphous four-compartment cycle (Fig.3) then there will be a symmetrical relationship:

$$R(xy) = \frac{K(13) \cdot X \cdot Y}{N + X} \cdot \frac{Y(m) \cdot (B/(Mm + B)) - Y}{Y(m)} \tag{4}$$

Note that Nn, the "Michaelis-constant" for the dependence of K(3) and C(m) on X is not necessarily equal to N, the "Michaelis-constant" for the dependence of R(xy) on X, and similar considerations apply to Mm and M.

Liebig's law seems to be exemplified by the cases, $Nn \ll X$, $M \gg B$; or, $Mm \ll B$, $N \gg X$, in which cases growth is directly proportional to one nutrient and independent of the other. It is however clear from equations 3 and 4 that these are limiting cases and that a full range of intermediate cases is computable. Mm and Nn play the roles of "coupling constants" between the two cycles. For $Mm \ll B$, changes in K(1) to K(10) will not affect the steady-state of the "W-cycle" and for $Nn \ll X$, changes in K(11) to K(20) will not affect the steady-state of the "A-cycle". If only one of these conditions is fulfilled e.g. $Nn \ll X$, then changes in K(1) to K(10) will affect the steady-state of the "W-cycle" but the resultant change in X will not further affect the "A-cycle". If however neither of these conditions is met then the coupled cycles will exhibit feed-back (Fig.4). The effects of changes of a given rate constant on the coupled steady-state can therefore be complex. For demonstration purposes the "A-

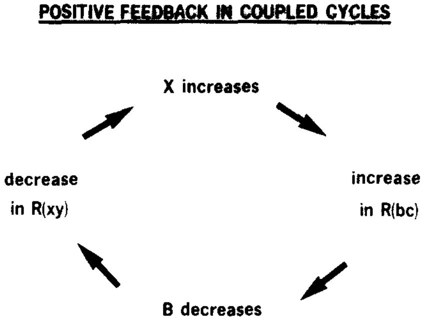

Figure 4. Positive feed-back loop in a two coupled four-box model.

cycle" is given the same numerical values as those of Table 2; the "W-cycle" is given values corresponding to a simplified version of the global nitrogen cycle (Table 3). Steady-state solutions were achieved by an iterative procedure. The plot shown is for deviation of K(18) from the standard value (calculated from R(wz) and W of Table 3) i.e. for a change in the rate of fixation of dinitrogen into organic forms. In Fig.5, an increase in the input from the abiotic reserve (i.e. additional nitrogen fixation) causes an increase in the nutrient pool of the "W-cycle" which then perturbs R(bc) (i.e. the rate of photosynthetic assimilation of carbon). Figure 5 is thus analogous to Fig.2 in which K(3) increases along the abscissa. Increase of Nn (the Michaelis constant of the assimilation rate of the "A-cycle" for X) increases the impact of changes in K(18) but in this figure Mm, the back-coupling coefficient is set equal to zero.. Figure 6 shows that, at low values of Mm, biomass nitrogen increases in a monotonic fashion in response to an increase in nitrogen fixation rate beyond a threshold value. However, at higher values of the coupling constant Mm, the increase in K(18) can cause a paradoxical decrease in the biomass nitrogen (Y).

Table 3. Standard values for a global nitrogen cycle

10^{15} moles or 10^{15} moles·y^{-1}		Definition	Reference
W	278600	atmosphere	Simpson 1977, Table 1
X	43	nitrate in oceans	Simpson 1977, Table 1 columns II–IV
Y	0.75	terrestrial biota carbon/80	Simpson 1977, Table 3
Z	23	organic + insoluble inorganic	Soderlund and Svensson 1976, Table 2
R(wx)	0.00053	atmospheric fixation	Delwiche and Likens 1977, Table 2
R(xw)	0.01617	R(wx) + R(wz)	
R(xy)	0.75472	(R(bc) – R(cb))*16/106	
R(yz)	0.75472	R(xy)	
R(wz)	0.01564	biological fixation of N	Soderlund and Svensson 1976, Figure 2
R(zx)	0.77036	R(yz) + R(wz)	

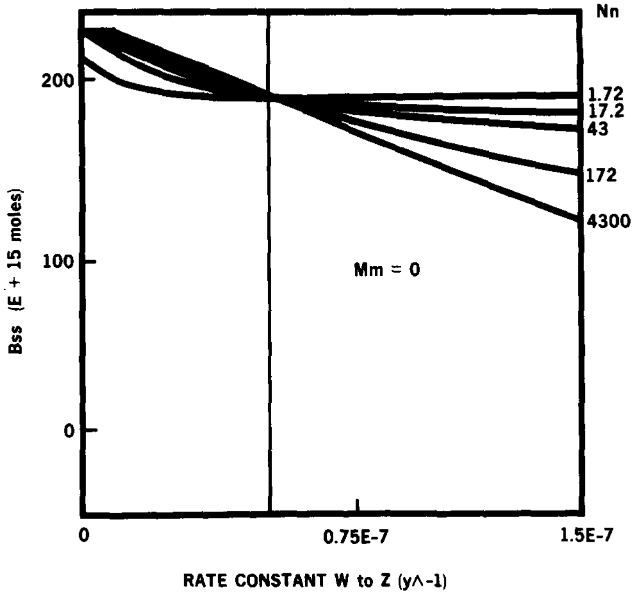

Fig. 5. Steady-state values of the nutrient pool of a global carbon cycle as a function of K(18). See Table 3 for the standard value of R(wz)/W indicated by the vertical line and Table 2 for the value of B indicated by the intersection of the curves with that line. The value of K(3) used is calculated according to equation 2 and K(13) is calculated by an analogous equation using the parameters of the "W-cycle", M = 200, C(m) = 75, N = 172, Y(m) = 4.5.

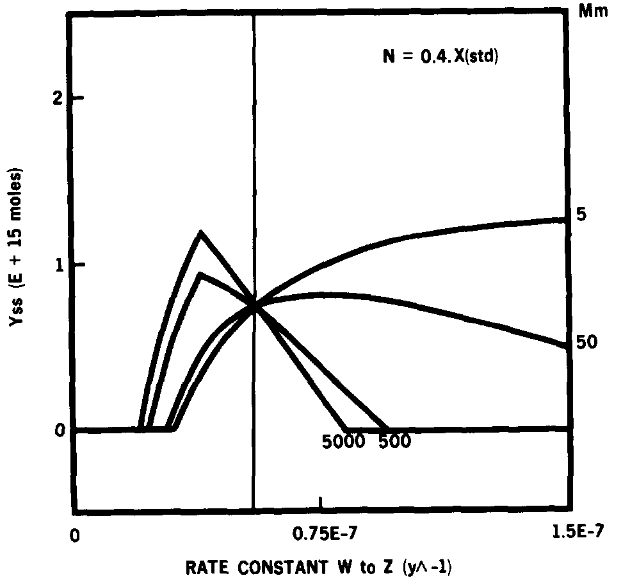

Figure 6. The influence of Mm (the Michaelis constant of nitrogen assimilation for nutrient carbon) on the response of Y (biomass nitrogen) to changes in K(18) (nitrogen fixation). Standard values as in Tables 2 and 3, M = 200, C(m) = 360, N = 17.2, Nn = 172, Y(m) = 4.5.

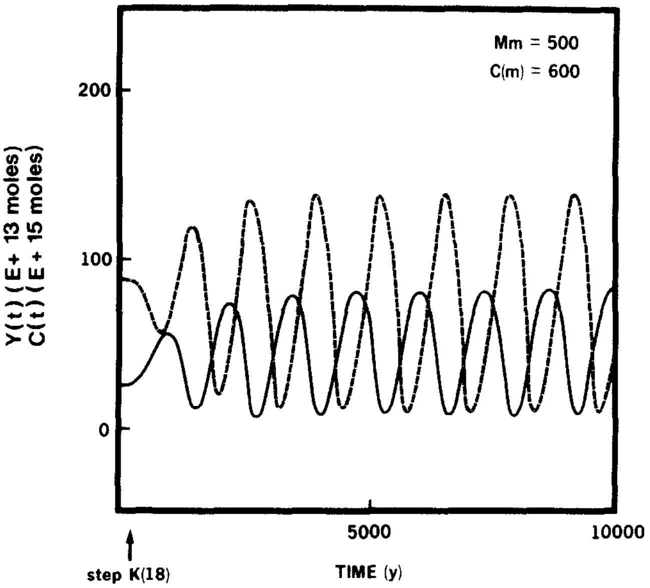

Figure 7. Time course of response of C (biomass carbon) (solid curve) and Y (biomass nitrogen) (dashed curve) to a step change of a rate constant for nitrogen fixation (K(18)). Other than K(18) all rate constants were calculated from the ratios of steady-state rates to pool sizes given in Tables 2 and 3. K(3) was calculated using M = 200, C(m) = 600; K(13) was calculated using N = 17.2, Y(m) = 4.5; Mm = 500, Nn = 43. The initial value of K(18) is $4.5 \cdot E\text{-}8y^{-1}$ and the new value (at t = 200y) is $6.0 \cdot E\text{-}8y^{-1}$ (the standard value from Table 3 is $5.614 \cdot E\text{-}8y^{-1}$).

The recognition that a system of two coupled four-box cycles exhibits positive feed-back (Fig.4) suggests that such a system may show complex kinetic behaviour. The numerical values of Tables 2 and 3 were used to compute time-dependent solutions of the system response to a step change in K(11) or K(18), i.e. the input of dinitrogen from the atmospheric compartment. A step increase in the nitrogen fixation rate of about one-third causes the system to go into sustained oscillation. (Fig.7). With different assumptions about the value of the forward coupling constant one obtains damped oscillation (Fig.8). As one would expect the value of the back coupling constant is also important. Higher values of Mm imply stronger coupling. Figure 9 shows that for otherwise identical conditions the value of Mm determines whether one obtains sustained or damped oscillations.

Interaction of two nutrient cycles. Stoichiometric constraints

The previous section has dealt with the coupling of two biogeochemical cycles by mass-action effects of the two nutrient pools of each cycle on the rate of biological assimilation in both cycles. In that section no restrictions were placed either on the ratio of the rates of net assimilation in the two cycles (R(bc)-

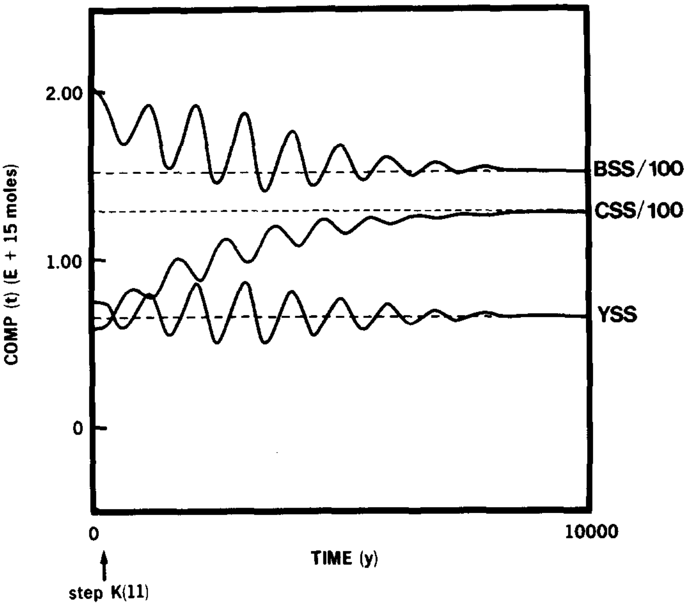

Figure 8. Time course of response of B (nutrient carbon), C (biomass carbon) and Y (biomass nitrogen) to a step change of the rate constant for nitrogen fixation into the nutrient pool, X, (K(11)). Other than K(11) all rate constants were calculated from the ratios of steady-state rates to pool sizes given in Tables 2 and 3. K(3) was calculated using M = 200, C(m) = 600; K(13) was calculated using N = 172, Y(m) = 4.5; Mm = 600, Nn = 172. The initial value of K(11) is 1.9·E-9y^{-1} (from R(wx) and W in Table 3). The new value (at t = 200y) is 2.155·E-8y^{-1} to give a 35% increase in the steady-state value of R(wx) + R(wz) (cf. Soderlund and Svennson, p.41).

R(cb))/(R(xy)-R(yx)) or on the ratio of two elements in the biomass pool (C(ss)/Y(ss)). It seems likely that such restrictions would in fact exist. Redfield [1934] proposed a constant stoichiometric relationship between C, N and P in marine plankton of 106/16/1 and these figures have been widely used in discussions of marine biogeochemical cycling. It is now recognised that the "Redfield ratios" may not apply to other ecosystems [Likens et al., 1981, Table 6.1] and there is currently debate among oceanographers about the constancy of this ratio for marine plankton [Peng and Broecker, 1984]. Although it is likely that Redfield ratios will vary between differing biomes and even between similar biomes at different times, nonetheless, the variability of elemental ratios is likely to be bounded [cf.Fig.10.3 of Hunt, Stewart and Cole, 1983]. The assumption of a fixed stoichiometric relationship (ϱ) between R(bc)-R(cb) and R(xy)-R(yx) can be modelled in the two coupled four-box system by completing the iterative calculation based on mass-action effects and then transferring molar units from C(ss) to B(ss) or from Y(ss) to X(ss) to achieve the desired stoichiometry (ϱ·K(15)/K(5)). The new values of B(ss) (or X(ss)) are then used to recalculate the steady-state which is again compared to the prescribed stoichiometry and the process re-iterated to any desired level of accuracy. A result is shown in

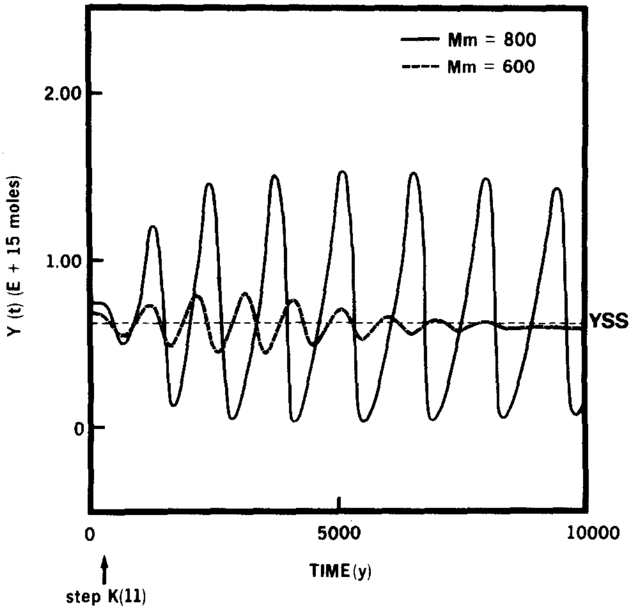

Figure 9. The influence of the back-coupling constant (Mm) on the time course of the response of Y (biomass nitrogen) to a step change in K(1). The curve exhibiting the strongly damped oscillations is taken from Fig.8. Similar conditions obtain for the higher amplitude curves except that Mm is increased from 600 to 800.

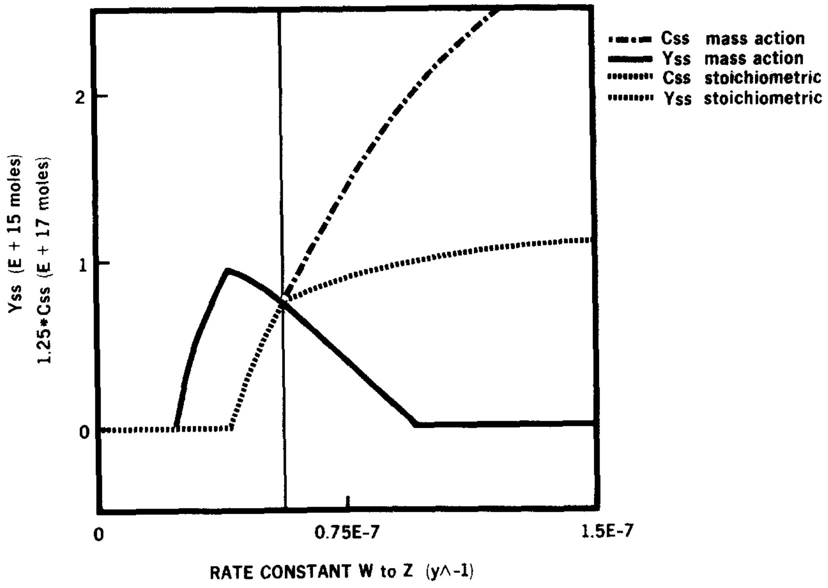

Figure 10. Stoichiometric constraints on positive feed-back effects in coupled nutrient cycles. Standard values as in Tables 2 and 3 and the legend to Fig.6, Mm = 500. For the plot under stoichiometric constraint the ratio of C(std)/Y(std) i.e. 80 is maintained at all values of K(18).

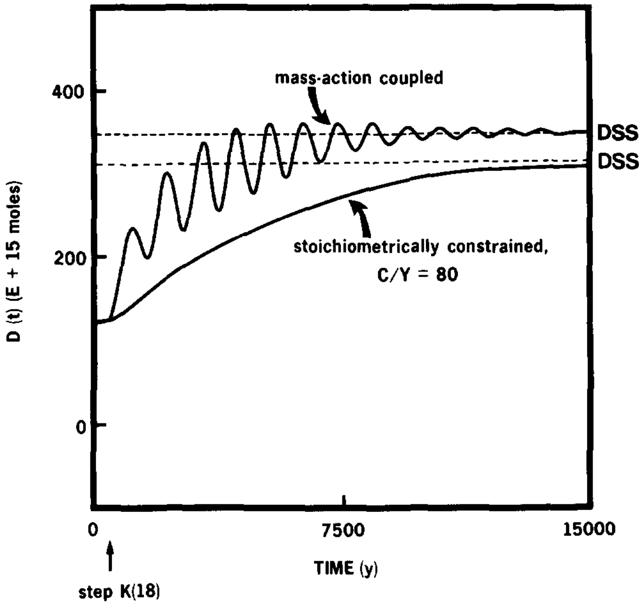

Figure 11. Stoichiometric constraints on the oscillatory behaviour of the two coupled four-box ecosystem. Conditions are as in Fig 7 except that Mm = 400 and, for the smooth curve, a fixed value of C(t)/Y(t) = 80 is maintained throughout the numerical integration procedure.

Fig. 10 where the sensitivity of the steady-state to perturbation of K(18) is shown for an unrestrained coupled system compared with a similar system of two coupled four-box cycles constrained to a C/N ratio of 80. The bimodal behaviour of the unrestrained system brought about by positive feed-back is transformed into a unimodal form.

The difference between stoichiometrically constrained and mass-action driven systems is shown even more clearly in time-dependent relationships. As in the case of the steady-state solutions, it can be shown that if the mass-action coupling implied by equations 3 and 4 is constrained by a fixed stoichiometrical relationship of elements in biomass then the kinetic response to a step change of a rate-constant is markedly modified. In Fig.11 the same initial conditions and values of all constants are assumed for both traces but the smooth curve arises from a calculation in which at each step of the Runge-Kutta procedure for numerical integration molar units of carbon or nitrogen are returned to the appropriate nutrient pool to preserve a C/N ratio of 80 [Simpson 1977, Table III]. In Fig. 12 molar units are spilled back to their respective nutrient pools if C/N < 60 or C/N > 120. The effect on kinetic behaviour clearly depends on the strictness of stoichiometric constraint and new emphasis is thus placed on the Redfield ratio as a determinant of ecosystem behaviour.

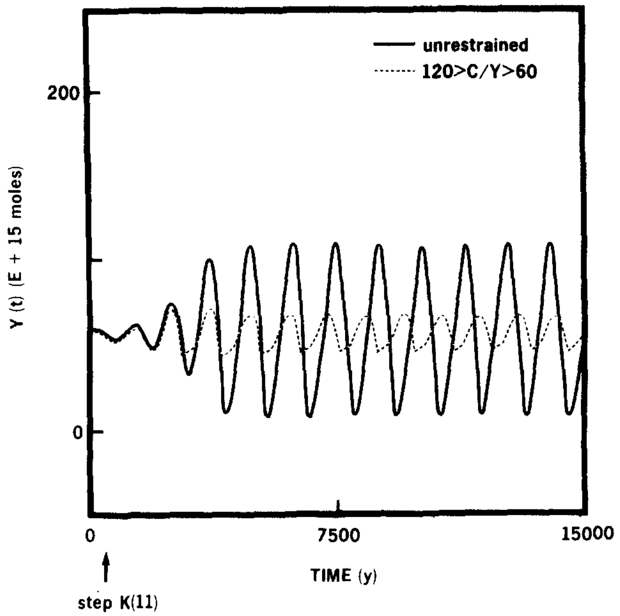

Figure 12. Stoichiometric constraints on the oscillatory behaviour of the two coupled four-box ecosystem in response to a step change in K(11). Conditions are as in Fig.7. The initial value of K(11) is 1.9·E-9y^{-1} (cf.Fig.8) and the new value (at t = 300y) is 5.76·E-9y^{-1} (giving a final total input rate from the inorganic reservoir close to that of Fig.7). The curve of lower amplitude was generated by imposing the condition $120 > C/Y > 60$.

Conclusion

The problem of how the biogeochemical cycles of different elements interact in any particular ecosystem is complex. A simple four-box model has been used to demonstrate that even models which recognize the complexities of natural ecosystems will nonetheless be inadequate for simulation if they fail to take into account the non-linear dependency of assimilation rate (gross primary productivity) upon nutrient concentration and biomass size. Representation of this process by a second-order equation is a step in the right direction but the inherent assumptions of an infinite Michaelis-constant for nutrient and an infinite carrying-capacity for biomass are unrealistic and should be corrected as in equation 1. These non-linearities become of particular importance in considering the interaction of two cycles. The Michaelis constants characterizing the dependence of the assimilation of one nutrient upon the other act as "coupling constants" determining the extent of feedback between the cycles.

The behaviour of the two coupled four-box system is also markedly dependent upon whether it is assumed that the interaction of the nutrient cycles is dominated by mass-action effects ("Liebig's law") or by stoichiometric constraints ("Redfield ratios"). Intermediate modes of behaviour can be generated if it is assumed that a range of atomic ratios can exist, as would presumably be the case in any natural ecosystem in which variation in species composition would be superimposed on intraspecific variability. For major biochemical elements (such as CHNOPS) infinite variability is improbable and the stoichiometry of assimilation is likely to be a major factor in the coupling of biogeochemical cycles.

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