On a Mathematical Model of the Carbon Cycle in Nature

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Abstract

A discussion is given of a simple mathematical model of the carbon dioxide cycle in atmosphere-biosphere-sea, with special attention to the possibility of self-sustained oscillations and to the behaviour of the cycle when additional carbon dioxide is injected from an outer source. The discussion is confined to phenomena with characteristic times of the order of 10—10⁸ years leaving out the long geologic periods as well as the purely annual periods. Some numerical computations are also carried out on the electronic computer BESK. The discussion and the computations show that self-sustained oscillations possibly appear due to the presence of the sea, and that they generally are favoured when there exist time-lags in the biosphere of the order of a few decades. The computations also indicate that additional carbon dioxide injected at a rate corresponding to the present combustion of fossil carbon does not change significantly the carbon dioxide concentration in the atmosphere, since most part of it will be stored in the biosphere. Thus, the present theory suggests that the increase of carbon dioxide indicated by recent measurements may represent part of a natural self-sustained oscillation and not necessarily be a response to an increased combustion of fossils.

I. Introduction

The circulation of carbon in nature has always been a topic of great interest to all natural sciences. Though present in comparatively small concentrations in the atmosphere, CO₂ is fundamental to all forms of terrestric organic life, which ultimately derive its carbon from this source. The yearly consumption of carbon due to the assimilation of plants is so great that, if not replaced at all, the present amount of carbon in the atmosphere would be depleated in a few decades. We have, however, a quasi-balance, in that carbon is given back to the atmosphere by respiration and decay at about the same rate as it is taken up. A small yearly drain is indicated by the presence of fossil carbon. In the long run, however, this drain is probably compensated by carbon coming from the interior of the earth, released in volcanoes and hot springs. When considering the yearly circulation these Tellus VIII (1956), 2

components can in any case be completely neglected. They become important only in connection with cycles involving geologic periods of time.

The reserve of carbon in the atmosphere is thus comparatively small. But carbon dioxide in the atmosphere is also in exchange with carbon dioxide dissolved in sea water, mainly as bicarbonate. This latter amount of carbon dioxide is very large compared to that in atmosphere. Thus, any depletion in the atmosphere would be compensated also by carbon dioxide delivered from the sea. The importance of this reservoir in the yearly circulation of carbon depends, of course, on the rate of exchange across the sea surface. This rate has been discussed recently by Nelson Dingle (1954) and Hutchinson (1954) and though opinions are rather conflicting, some information exist. The important question seems to be, however, if the rate of overturning of sea water is great enough to

permit an efficient exchange with the whole volume of sea water (CALLENDAR, 1938, KULP, 1953, WORTHINGTON, 1954).

At the present time another source of carbon in the atmospheric exists, namely, the carbon dioxide released by the combustion of fossil carbon. The total amount delivered to the atmosphere in the last fifty years has been estimated to about ten per cent of the quantity present. Callendar (l.c.) raised the question to what extent such an amount released in the atmosphere might affect the radiation balance and thus also the climate of the earth. Carbon dioxide is of importance in this connection as it absorbs some long wave radiation. To answer this question, we must, however, first know if the carbon dioxide released by combustion of fossil carbon causes a corresponding steady accumulation of carbon dioxide in the atmosphere or if it is essentially compensated by increased assimilation or by absorption in the sea. The data on carbon dioxide concentration in the atmosphere used by Callendar as an argument for the increase are, however, too scattered in time and space to make a definite decision on this point possible. In fact, it may require a period of collection of many decades to detect any real trends in the concentration of atmospheric carbon dioxide. Now, even if we obtain a positive evidence of an increase we do not know for certain that this can be attributed to the combustion of fossils. In the natural cycle of carbon there may well appear oscillations which are not generated by external forces but are of a self-sustained type. Therefore, before one attempts to draw any conclusions concerning the influence of fossil carbon combustion from experimental data one should also know something about the possibility for the appearance of such selfsustained oscillations.

One main object of the present paper is to investigate these questions by help of a mathematical model, which is supposed to picture at least the main features of the carbon cycle in the system atmosphere-biosphere-sea. The discussion is confined to phenomena with characteristic times of the order of 10—10³ years, leaving out the long geologic periods as well as the purely annual periods. The authors are well aware of the limitations of such a model as the one presented here, and

certainly we do not claim that it can be used for a quantitative prediction of any actual changes in the concentration of atmospheric carbon dioxide. However, we think that already this crude model can give some valuable information about the characteristic dynamics of the carbon cycle and, in particular, information on the possibility of selfsustained oscillations. As will be seen from the investigation, the characteristic dynamics of the cycle is in the main related to some few qualitative features of the system and does not depend critically on its detailed structure. This is, of course, of essential importance when dealing with a problem where both the theoretical and experimental knowledge is still so meagre that the details of any specific mathematical model might be questioned.

The mathematical method to be used is well-known in the branch of "non-linear mechanics". It is a very illustrative quasi-geometrical method, which has found much use in applied mechanics and electronics, and it seems also to be a promising tool when tackling many cyclic problems in geo-chemistry and biology.¹

The theoretical results are illustrated by some numerical computations for a specific model. These computations were performed by help of the electronic computer BESK in Stockholm.

General conclusions drawn from the theory and from the computations are found in the last section.

II. Basic assumptions

From existing quantitative data it may be inferred that processes which are of importance in the natural short-time circulation of carbon are those listed below.

- Assimilation of carbon by the terrestrial plants.
- 2. Respiration (production of CO₂ by terrestrial plants).
- 3. Transition of living organic material to dead organical material.
- 4. Decay of dead organic material to carbon dioxide.
- 5. Exchange of carbon dioxide between the atmosphere and the oceans.

¹ Some general aspects on the application of the method to problems in hydromechanics, geo-chemistry and biology will be presented in a forthcoming paper by one of the authors.

Processes which will be neglected are:

- Production of juvenile and cyclic carbon by volcanoes.
- 7. Accumulation of fossil organic matter.
- 8. Weathering of rocks by the action of carbon dioxide.
- 9. Assimilation-respiration processes in sea water.

The amounts of carbon involved in the neglected processes (6)—(8) are relatively small and of importance only in phenomena with very large characteristic times, say 10⁵ years or more. The process (9) can be regarded as an internal affair in the sea, although it involves considerable amounts of carbon. The cycle is very rapid and probably well-balanced and cannot have any essential dynamic influence in the problems considered here.

In the construction of the model some simplification must be introduced, for mathematical reasons. The circulation system to be considered here is pictured schematically in fig. 1. It involves four basic storage units between which carbon is transferred. The four storage units represent the terrestrial assimilating plants, the dead organic matter, the atmosphere, and the sea. Between these units carbon is transferred by the processes listed. The quantities x_l , x_d , y_a and y_s written in the boxes denote the corresponding total stores of carbon. They are the dependent variables of our mathematical model.

The next step is now to make reasonable assumptions concerning the transfer rates of these quantities. As to assimilation it has repeatedly been demonstrated that the rate of assimilation of a variety of plants depends on the concentration of CO₂ in the air (cf. Lundegård, 1924, 1954) when none of the other growth factors (light, moisture, temperature, nutrients etc.) are limiting the growth.

Early experiments by STÅLFELT (1924) demonstrated clearly that both spruce and pine increase their assimilation proportionally to the increase of CO₂ in the air. Most experiments, however, have been conducted on annual plants. Especially the recent extensive work by THOMAS & HILL (1949) deserves to be mentioned. The experiments were carried out both in the field and in greenhouses under fairly normal conditions with respect to other growth factors. They found, as example, that Tellus VIII (1956), 2

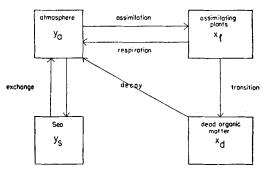


Fig. 1. Simple model of the carbon cycle in nature.

the assimilation of CO₂ in alfalfa, in sugar beets and tomatoes increased linearly with the CO₂ concentration of the air up to twelvefold the normal concentration of CO₂.

It is obvious that the rate should furthermore be proportional to the mass of the assimilating plants x_l , and specifically to the mass of the green parts where most of the metabolic processes take place. The mass of the green parts can, however, be taken to be proportional to the total mass of the plants. Plants also respire, thereby giving back CO_2 to the air, and this rate should also be proportional to the mass of the plants. The rest of the CO_2 assimilated is stored in the plants, mostly in structural elements.

At this stage, however, a distinction must be made between annual and perennial plants, annual plants being represented by those whose green parts die and decay after an assimilating season due to drought or frost. We are here interested in the dynamic behaviour of the carbon cycle with respect to a sequence of years, hence these annual plants cannot contribute significantly to this behaviour. Even if there is an accelerated growth of the annual plants due to an increase of CO₂ in the atmosphere there will be an equally increased rate of decay and no net changes in x_i . Annual plants will for this reason be left out of consideration in the following. The mass of assimilating matter referred to later on is represented solely by the perennials which for all practical reason are represented by forest

Further, we have the drain process, transferring living organic matter to dead organic matter. As a first approximation one can put also this drain proportional to the mass of the assimilating plants. This seems to be fairly correct when one discusses changes with characteristic times which are long compared to the life-time of the plants. In other cases, one has to take into account the time-lag effect, which can be supposed to influence the dynamics of the system essentially. The discussion of this is, however, postponed till Section VII.

Thus, as a very simple approach we can write

$$\frac{dx_i}{dt} = k_1 x_i \gamma_a - k_1' x_i - k_2 x_i$$

where k_1 , k'_1 , k_2 are constants determining the intensity of assimilation, respiration and drain to dead material, respectively.

Looking at the geometric representation of the equation in an $x_l - y_a$ plane, the derivative $\frac{dx_l}{dt} = 0$ would be represented by the y_a -axis $(x_l = 0)$ and by a line $y_a = \frac{k_1' + k_2}{k_1}$ parallel to the x_l -axis (See fig. 2, full-drawn thick line) and the general isolines of this derivative are hyperbolas to which these straight lines are asymptotes.

The assumptions underlying the rate equation above may hold in the near vicinity of $y_a = \frac{k_1' + k_2}{k_1}$ It is, however, unlikely that the

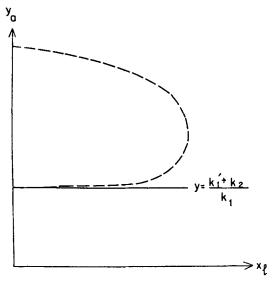


Fig. 2. For explanation see the text.

rate would be so simply related to y_a at higher values of y_a . The simple formula really implies that for y_a greater than the equilibrium value, x_l would always increase. Firstly, x_l cannot increase without limit for pure spatial reasons. Secondly, as is obvious from the discussion in the appendix, an increase in y_a seems merely to rise x_l to a higher equilibrium value. It is conceivable, and has also been observed, that very high CO_2 concentrations will retard the growth and finally kill the plants, the upper limit being around 1 per cent by volume (Ballard, 1941). Though such concentrations at present time are inconceivable it may be well worth for the general picture to take this upper limit into account.

Thus, we must expect $\frac{dx_l}{dt}$ = 0 for sufficiently large values of y_a as well as of x_l , and the combined limiting effects would give us a curve of $\frac{dx_l}{dt}$ = 0 like the dashed line in fig. 2. For small x_l the equilibrium value of y_a should be nearly independent of x_l and the curve should then be practically horizontal.

It is now easy to sketch the appearance of the isolines in case of the more general equation.

$$\frac{dx_1}{dt} = f(x_1, y_a)$$

and we arrive at the picture of fig. 3. It is seen that $\frac{dx_1}{dt}$ is positive inside the closed region and negative outside.

The behaviour of our system is apparently critically dependent on the relationship between assimilation and y_a . A question which arises in this connection and which deserves some discussion is whether there exist other limiting growth factors which can critically change the assumed relationship. Some of the experimental investigations referred to can possibly be critisized because of the fact that they were carried out when other growth factors, notably the nutritional ones, were at an optimum. Nutritional factors which have been shown to influence the assimilation are notably nitrate and phosphate. The experiences of these factors come mainly from agriculture where nitrate and phosphate fertilizers frequently give high responses in crop growth. Under uncultivated conditions there is, however, a

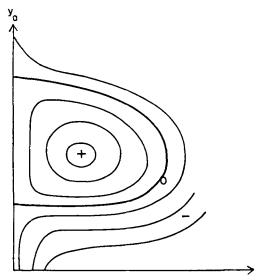


Fig. 3. General appearance of the function $f(x_1, \gamma_a)$ in the $x_1 - \gamma_a$ -plane.

normal return of these two aliments to the soil so there is a quasi-balanced cycle between the plants and soil. There is, of course, some loss especially of nitrate in drainage water but on the other hand there is also an addition from the atmosphere. Considering also the great expanse of leguminous plants the nitrate does not seem to be of such an importance as a limiting factor. Furthermore, it is obvious from the geographical distribution of plant communities that there exists an ecological selection of plant species operating in such a way, that nutrient conditions seldom become limiting. For instance, spruce forests which have a rather low demand on nitrogen will grow on a highly leached soil, low in soluble nitrates.

Other growth factors are temperature and moisture. These will mainly influence the areal distribution of plants, the precipitation being of greatest importance where temperature is at an optimum and vice versa. It is apparent that only the borders of our plant communities are really limited by these two factors, not the interior of vegetation-covered areas. These borders are mainly occupied by annual plants which are not considered here. Since, furthermore, changes in both temperature and precipitation pattern are presumably slow as compared to the characteristic times of our sy-Tellus VIII (1956), 2

stem (compare length of glaciation periods) it is hardly any need to discuss them further

Another objection can, however, be raised here against the assumptions made, namely that an increase in assimilation due to an increase of CO2 in the atmosphere may decrease the life time of the plants so that no net increase in the mass x_i would take place. One may, for instance, think that the mature state of a tree is related to its mass, in which case the objection appears to be well-founded. The age limit of perennials is a very interesting though apparently complicated question about which systematic observations seem to be lacking. The embryonic cells in growing points and growing areas (cambium) of a tree seem themselves to have an ability for eternal life as long as they are in a state of repeated divisions. In this respect they are similar to the embryonic cells in the sexual organs of animals. The cells in a tree which are left behind the growing areas do not live long but are converted into structural units which, as long as they are not attacked by parasitic organisms, seem to escape the decay processes. From these points of view there would be no age limit for a tree. The limiting factors are, however, considered to be the slowly decreasing ability for transport of water, salts and assimilation products between the root and the top of the tree (increasing path of transport). (cf. STRASSBURGER et al 1944 p. 228). Thus the height of a tree may finally put a limit to a proper functioning. Carbon dioxide can, however, not be expected to favor the height growth in particular, this is goverened rather by the light factor, as can be observed for instance in a spruce forest. For that reason one would not expect an intimate inverse relation between the carbon dioxide and the average life time of a tree. Further, another factor which is probably more important for the age limit of trees is the attack of parasites, both insects and microorganisms on living trees; the probability of such an attack must increase with the age of a tree somewhat in that manner pictured in the appendix.

Finally, even if the average life time should decrease due to an increased CO₂ in the atmosphere, there must be a time lag involved which in any case would favor the instability

of the whole dynamic system, giving rise to self-sustained oscillation of the type discussed in Section VII.

The next process to consider is the rate of change of dead organic matter. The dead organic matter is drained by decay processes. These processes are performed by all animals, bacteria, fungi and all saprophytic plants. This drain into the atmosphere has been listed as decay but is actually a respiration process as practically all decay takes place through metabolic processes in which a series of species feed on each other. Neglecting at present the effect of a time-lag in the living matter it is clear that this rate should be a function of both x_l and x_d as the loss of CO₂ to the atmosphere should be dependent essentially on x_d . For small values of x_l and x_d it is then conceivable that the rate can be written

$$\frac{dx_d}{dt} = k_2 x_1 - k_3 x_d$$

It is, however, probable that the proportionality constant k_3 is less at higher x_d than at lower. A great accumulation of organic matter would decrease the rate at which oxygen can enter in the decay process. Therefore we should more generally put

$$\frac{dx_d}{dt} = g(x_l, x_d)$$

where $g(x_l, x_d) = 0$ in the $x_l - x_d$ -plane forms a straight line near origo but curves upwards further away. This line and the other isolines are sketched in fig. 4. As to the sign of $\frac{dx_d}{dt}$ it must be positive to the right of the line $g(x_l, x_d) = 0$ and negative to the left of it.

Finally, considering the rate of exchange between the atmosphere and the sea, which is a purely physical process, we can write for the rate of change of γ_s

$$\frac{d\gamma_s}{dt} = k_4(\gamma_a - k_5\gamma_s)$$

where k_5 is equivalent to an equilibrium constant, and k_4 is a proportionality constant $\left(\frac{1}{k_4}\text{equals the characteristic time of adjustment}\right)$. This equation is equivalent to the expression

$$\frac{dQ}{Adt} = E(P - p)$$

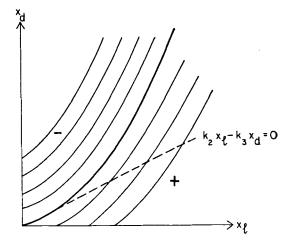


Fig. 4. General appearance of the function $g(x_l, x_d)$ in the $x_l - x_d$ plane.

where P - p is the pressure head at the interface, E is the invasion constant and A the area. In our case the amounts involved are expressed in mg \times cm⁻² of the earth's surface.

The value of E has been determined experimentally by several scientists with much varying results depending upon the experimental conditions. The best value according to HUTCHINSON (1954) is that obtained by BOHR (1899) which is 0.25 mg \times cm⁻² \times atm.⁻¹ min.⁻¹. Using this value and the values of γ_a and γ_s listed in Table 1, k_4 becomes $6 \times 10^{-2} \times \text{year}^{-1}$.

In the exchange between the sea and the atmosphere there is a possibility that due to the circulation of sea water a certain time delay in the exchange takes place. This is, of course, of greatest importance when the deep water is involved. Carbon dioxide, taken up in the polar regions may be carried down into the deep water and is then transported south to the upwelling regions. In the meantime a change of the carbon dioxide content of the atmosphere may have taken place, thus upsetting the original dynamic equilibrium. It would be of great interest to study the effect of such a time delay to our system, but this will involve a great deal of mathematical labour. Clearly, to obtain results of interest one must take into account the biosphere as well as the atmosphere in the picture, and that will lead to

a fourt-hordersystem, even with the simplest possible kind of lag-operator. For this reason, the discussion of the time-lag in the sea has been postponed. On the other hand, we will in Section VII take up a discussion of the time-lag in the biosphere, which seems to be a still more important factor. Introducing finally the total amount of carbon dioxide a in our cycle, assumed here to be constant, the system of equations describing the cycle will be

$$\frac{dx_{l}}{dt} = f(x_{l}, y_{a})$$

$$\frac{dx_{d}}{dt} = g(x_{l}, x_{d})$$

$$\frac{dy_{s}}{dt} = k_{4}(y_{a} - k_{5}y_{s})$$

$$x_{l} + x_{d} + y_{a} + y_{s} = a$$
(1)

We next wish to examine the dynamic characteristics of this system. Do stable equilibrium values exist and in which manner are such stable equilibria approached? If there are unstable equilibrium points, is it then possible to get steady self-sustained oscillations around these? These are questions we want to answer in the following.

III. Quantitative data

Before discussing the dynamic behaviour of the system described by the equations in (1) some estimates of the present quantities will be listed. The amounts in Table 1 are expressed in mg cm_e⁻² (cm_e² = cm² of the earth's surface). The data are taken from HUTCHINSON (1954) except the figure for x_1 which has been estimated from the yearly assimilation, from the percentage assimilation by forests shown in Table 2 and from an estimated average life time of 50 years.

Table 1

The values for x_l , x_d and assimilation rate are, of course, subject to uncertainties but are definitely of the right order of magnitude.

It may also be interesting to know the area distribution and assimilation percentage of different plant groups. The values in Table 2 are computed from the table on p. 379 in HUTCHINSON'S paper (1954).

Table 2

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	Per cent of total assim- ilation	Per cent of total land area
Forests		35
Cultivated	29	21
Grassland	13	25
Desert	0.4	19

It is seen that the forest vegetation is rather dominating in the yearly assimilation.

IV. The system atmosphere-biosphere

We will start the mathematical discussion for a simplified system, where the sea is left out of consideration. It is supposed that the essential dynamic character of the system is governed by the remaining part, comprising the atmosphere, the assimilating plants and the dead organic matter, and that the sea merely acts as an extra damping factor. Anyway, it is instructive to start with this simpler case and get acquainted with the mathematical method of discussion before we tackle the more complete system.

The system is described by the set of equa-

$$\frac{dx_l}{dt} = f(x_l, y_a)$$

$$\frac{dx_d}{dt} = g(x_l, x_d)$$

$$x_l + x_l + y_l = g$$
(I a)

The functions $f(x_l, y_a)$ and $g(x_l, x_d)$ have been discussed earlier, and their general appearance is seen in figs 3—4.

Eliminating y_a by help of the last equation we get

$$\frac{dx_l}{dt} = f(x_l, a - x_l - x_d)$$

$$\frac{dx_d}{dt} = g(x_l, x_d)$$
(1 b)

Our geometrical discussion is now carried out in an $x_1 - x_d$ -plane. See fig. 5. In this plane, $y_a = 0$ is represented by the line $x_1 + x_d = a$ (dashed line) while $y_a = a$ is represented by origin. The appearance of the

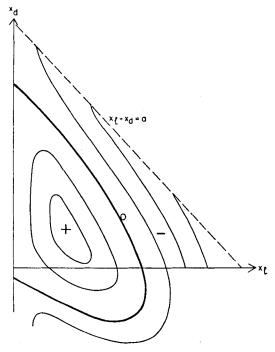


Fig. 5. The function $f(x_l, a-x_l-x_d)$ in the x_l-x_d plane.

curve $f(x_l, y_a) = 0$ and the other isolines of that function will be seen from the figure. The curves from fig. 3 are obviously turned upside down and distorted. Increasing or decreasing the value of a will just mean a translation upwards or downwards of the whole isoline pattern. Since x_l , x_d and y_a must be positive, the region of existence is the triangle bounded by the line $x_l + x_d = a$ and the coordinate axes.

Assume now that we start from a specified state of the system and follow the development in time as determined by the above equations (Ib). In our geometrical picture the actual state corresponds to a point (x_l, x_d) , and the time development is represented by a certain trajectory generated by this point during its motion.

The direction of the general trajectory field is easily sketched with the aid of the equations

(1 b) and the appearance of the functions f and g shown in figs. 3-4. On the curve f=0 the trajectories run vertically, on the curve g=0 horizontally. Inside the closed lope of the curve f=0 the trajectories are directed to the right, outside that curve to the left. Furthermore, they are directed upwards to the right of the curve g=0, downwards to the left of that curve. See fig. 6. The exact direction of the trajectory in each point can be found from the expression

$$tg \alpha = \frac{dx_d}{dx_l} = \frac{g(x_l, x_d)}{f(x_l, a - x_l - x_d)}$$

obtained by dividing the equations in (1 b). The above method will, however, not work well in the vicinity of the points where f = 0 and g = 0 simultaneously, since the direction will then be indeterminate. These points are obviously equilibrium points, since

$$\frac{dx_l}{dt} = \frac{dx_d}{dt} = 0,$$

and they must be investigated separately by an analytical method.

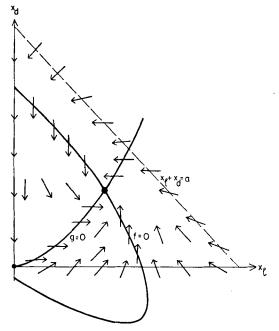


Fig. 6. The functions $f(x_l, a-x_l-x_d) = 0$ and $g(x_l, x_d)x = 0$, equilibrium points and trajectory directions in the x_l-x_d plane.

In the neighbourhood of an equilibrium point x_{l_0} , x_{d_0} , the functions f and g can be developed in a Taylor series and approximated to

$$f = \alpha \cdot \xi + \beta \cdot \eta$$
$$g = \gamma \cdot \xi + \delta \cdot \eta$$

where

$$\xi = x_l - x_{l_0}$$
$$\eta = x_d - x_{d_0},$$

and

$$\alpha = \left(\frac{\partial f}{\partial x_l}\right)_{x_d = \text{const.}}, \quad \beta = \left(\frac{\partial f}{\partial x_d}\right)_{x_l = \text{const.}}$$

$$\gamma = \frac{\partial g}{\partial x_l}, \quad \delta = \frac{\partial g}{\partial x_d}$$

$$(2)$$

are partial derivatives at the equilibrium point.
(1 b) can then be written

$$\frac{d\xi}{dt} = \alpha \cdot \xi + \beta \cdot \eta$$
$$\frac{d\eta}{dt} = \gamma \cdot \xi + \delta \cdot \eta$$

and putting

$$\xi = \xi_0 e^{\lambda t}$$
$$\eta = \eta_0 e^{\lambda t}$$

where λ is a complex frequency, we get the frequency equation

$$\begin{vmatrix} \alpha - \lambda & \beta \\ \gamma & \delta - \lambda \end{vmatrix} = 0$$

or

$$\lambda^2 - (\alpha + \delta)\lambda + (\alpha\delta - \beta\gamma) = 0$$
 (3)

If the real parts of the roots are both negative, the equilibrium point is stable and all trajectories in the neighbourhood of the equilibrium point approach it when $t \to +\infty$, otherwise the solution is unstable and at least some trajectories in the neighbourhood will depart from it when $t \to +\infty$.

A more detailed classification of the equilibrium point according to the appearance of the trajectory field in the neighbourhood is found in fig. 7.

The criterion for negative real parts of the roots is now

$$\alpha + \delta < 0$$
 $\alpha \delta > \beta \gamma$ (4)

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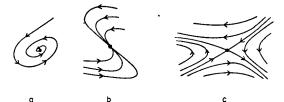


Fig. 7. Trajectory field near equilibrium points:

a) focal point (complex roots).

b) nodal point (real roots of the same sign), and c) saddle point (real roots of opposite sign).

The local and nodal points can be stable (as in the figure) or unstable, the saddle points are always unstable.

According to our previous assumptions $g(x_l, x_d)$ is an increasing function in x_l but a decreasing function in x_d . Thus $\gamma > 0$, $\delta < 0$. As to α and β the regions where these are positive and negative are shown in fig. 8 a and 8 b. In fig. 8 c is shown the stability or instability of the equilibrium point according to its position on the curve f = 0. We can follow the changes by varying a from small to large values, corresponding to a translation of the curve f = 0 upwards from a position where the closed loop lies wholly under the x_l -axis. For very small a there is only one equilibrium point on the x_d -axis, and it is stable. This means that no living plants can exist, and all carbon dioxide is in the atmosphere. Increasing a so that O falls between A and B will give us two equilibrium points, one unstable on the branch AB and one stable on the branch BD. Thus, when a certain minimum total amount of carbon dioxide is available, living plants can develop and the plant mass will increase until a new stable equilibrium is reached. For still larger a we come, however, over to the case of three equilibrium points, one stable on OA, one unstable on AD and one stable on BD, and ultimately we arrive again at the case of one single stable point, now on the branch OA. The two last cases have, however, only theoretical interest, since such a-values as is required cannot possibly appear. The separation point D is the point where the curve g = 0 is tangent to the curve f = 0. In this case

$$\left(\frac{dx_d}{dx_l}\right)_{l=0} = \left(\frac{dx_d}{dx_l}\right)_{g=0}$$

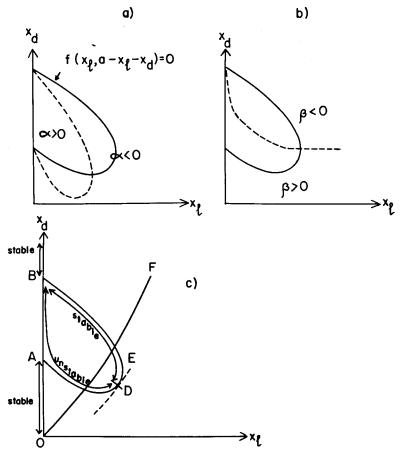


Fig. 8. Regions of stability and instability of equilibrium points on $f(x_1, a-x_1-x_d)=0$.

or
$$\frac{-\left(\frac{\partial f}{\partial x_l}\right)_{x_d - \text{const.}}}{\left(\frac{\partial f}{\partial x_d}\right)_{x_l - \text{const.}}} = \frac{-\frac{\partial g}{\partial x_d}}{\frac{\partial g}{\partial x_d}}$$

or

$$\alpha\delta = \beta\gamma$$

which is seen to be the limiting form of the second stability condition in (4).

From quantitative date it is immediately inferred that the second case, with one root on AB and one root on BD, represents the present conditions on the earth. The exact position of the actual equilibrium point on BD is, of course, not known. We cannot even assume that the present state is close to the equilibrium point.

As to the oscillatory character of the solution in the vicinity of an equilibrium point, this is determined by the discriminant to the frequency equation:

$$D = (\alpha + \delta)^2 - 4(\alpha\delta - \beta\gamma) = (\alpha - \delta)^2 + 4\beta\gamma$$

When this is positive the changes are exponential (nodal point or saddle point), when it is negative the changes are oscillatory (focal point). We find that the changes are exponential near the equilibrium points at origin, but that the changes are oscillatory on the relevant branch BD at least down to the point of vertical tangent E. After this discussion it is easy to sketch up the whole trajectory field. The result is demonstrated in fig. 9 for the case of actual interest, where we have one stable and one unstable equilibrium point.

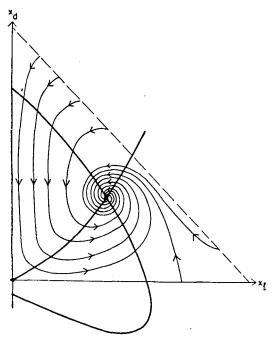


Fig. 9. Trajectory field in the $x_1 - x_d$ plane in the normal case.

Since the speed of the representative point is

$$\nu = \sqrt{\left(\frac{dx_l}{dt}\right)^2 + \left(\frac{dx_d}{dt}\right)^2} = \sqrt{f^2 + g^2}$$

the geometric picture will give the full information about the dynamical behaviour of the system.

V. Effect of an external source

We next consider the effect of an external source releasing carbon dioxide in the atmosphere at a constant rate q, representing the combustion of fossil carbon. Fossil carbon is a component in the long-time geologic cycle and has been neglected since its rate of transfer is very small as compared to those considered in our model. However, this is only true when the cycle is driven naturally. The combustion of fossil carbon represents, on a geologic time-scale, an extremely violent transient forced upon the system, and can during some shorter time affect also the more rapid cycle in which we are interested.

Mathematically, this external source will not change our basic equations, except that the Tellus VIII (1956), 2

constant a is replaced by a linear function a+qt. The previous description in terms of trajectories will, however, not be applicable now, since the direction of a trajectory is not given uniquely as a function of space. Nevertheless, some qualitative results can be obtained by simple geometrical considerations, at least for small values of q. If q is very small the system will be almost in equilibrium all the time (provided no self-sustained oscillations occur). Confining to the simple case, where the sea is left out of account, the equilibrium point is given by the cut between the curves $f(x_l, a - x_l - x_d) = 0$ and $g(x_l, x_d) = 0$ in fig. 9. An increase in a by the amount qt corresponds in the figure to a vertical displacement of the line $x_l + x_d = a$ and the curve f = 0 by the distance qt, and the change in y_a equals the change in the distance from the equilibrium point to this line. See fig. 10.

Obviously y_a is almost constant as long as we are on the straight-lined part of the curve f = 0, and the increase of a is distributed between x_l and x_d .

When q is not very small, transient oscillations will be superimposed upon the previous solution. These oscillations are most pronounced at the start of the injection but they are generated to some degree all the time by the non-linearities of the system. Still more important is, however, the appearance of a quasi-constant displacement of the y_a -value

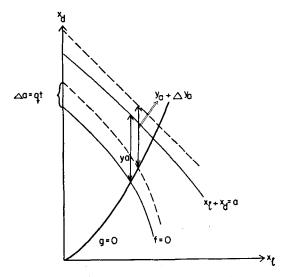


Fig. 10. The shift of the equilibrium point due to an external source of carbon dioxide.

from the static equilibrium, the amount of which can also be estimated from the figure. Assuming that due to the injection of CO_2 the equilibrium values of x_l and x_d are changed by amounts Δx_l and Δx_d during unit time, then the actual state is represented by the cut between the isolines $f = \Delta x_l$ and $g = \Delta x_d$ (second order terms neglected) and a corresponding small increase appears in y_a . Finally, if the natural system performs self-sustained oscillations, one should expect that these should just be superimposed on the previous picture. These effects will be demonstrated later on in some numerical examples.

The essential result is, however, that in this model any artificial increase of CO₂ in the atmosphere will be strongly damped by the action of the biosphere.

It might be noted that HUTCHINSON (1949) has reached the same conclusion from a more qualitative reasoning. His argument is the following (p. 227): "The rate of industrial production is therefore of the order of I per cent of the rate of biological production on land. Assuming the validity of CALLENDAR'S conclusion that transport through the sea is not involved, — it is necessary also to suppose that the mechanism of the biosphere is such that a very accurate regulation occurred during the nineteenth century, but that during the twentieth an increase of the order of I per cent in the total production of CO₂ was quantitatively rejected by the system. This is extremely improbable."

VI. The system of atmosphere—biosphere —sea

We now want to take up to discussion the more general case where also the sea is included. The full system (1) will be, after elimination of y_a ,

$$\frac{dx_{I}}{dt} = f(x_{I}, a - x_{I} - x_{d} - y_{s})$$

$$\frac{dx_{d}}{dt} = g(x_{I}, x_{d})$$

$$\frac{dy_{s}}{dt} = k_{4} [a - x_{I} - x_{d} - (1 + k_{5}) y_{s}]$$
(1 c)

Again, we consider only the upper branch BD of the curve f = 0 as represented in fig. 9. This is quite reasonable, considering the amount

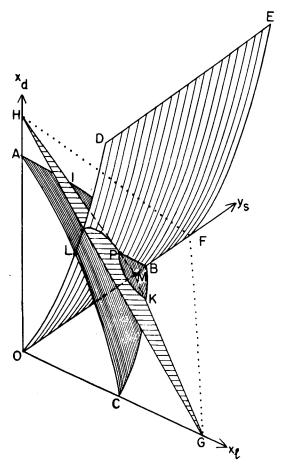


Fig. 11. Surfaces of $\frac{dx_l}{dt} = 0$, $\frac{dx_d}{dt} = 0 \text{ and } \frac{dy_s}{dt} = 0 \text{ in the } x_l - x_d - y_s \text{ space.}$ The points P and M are equilibrium points.

of carbon available in the sea. It has been experimentally shown that plants can stand carbon dioxide concentrations as high as one per cent, i.e., 30 times the present concentration. From table I we infer that such an increase in the atmosphere would require practically all carbon in the sea to be given up, a physical impossibility. Thus the lower branch of the curve f=0, where the choking of the plants appears, is not relevant here. In fig. 11 this system is pictured in an $x_1 - x_d - y_s$ -space. The surface ABC together with the $x_d - y_s$ -plane then represents the surface f=0, DEFO the surface g=0 and finally HMG the plane

 $a-x_l-x_d-(1+k_b)\gamma_s=0$, on which surfaces $\frac{dx_l}{dt}=0$, $\frac{dx_d}{dt}=0$ and $\frac{dy_s}{dt}=0$, respectively. These surfaces cut in the points M and P which are then the equilibrium points. The plane HFG represents $\gamma_a=0$, i.e. $x_l+x_d+\gamma_s=a$. This plane and the coordinate planes bound the region of existence of our solution.

Also in this three-dimensional space the trajectory field can be constructed, using a technique similar to the one described earlier.

The frequency equation corresponding to this more general case is easily derived from (1 c), it becomes

$$\begin{vmatrix} \alpha - \lambda & \beta & \beta \\ \gamma & \delta - \lambda & o \\ -k_4 & -k_4 & -k_4(\mathbf{I} + k_5) - \lambda \end{vmatrix} = 0$$

where α , β , γ and δ are the quantities defined earlier. It is to be noted that $\frac{\partial f}{\partial \gamma_s} = \frac{\partial f}{\partial x_d} = \beta$.

Developing the above determinant gives us the equation

$$\begin{split} \lambda^{3} + \left[k_{4} \left(1 + k_{5} \right) - \left(\alpha + \delta \right) \right] \lambda^{2} + \\ + \left[\alpha \delta - \beta \gamma + k_{4} \beta - k_{4} \left(1 + k_{5} \right) \left(\alpha + \delta \right) \right] \lambda + \\ + k_{4} \left(1 + k_{5} \right) \left(\alpha \delta - \beta \gamma \right) + k_{4} \left(\gamma - \delta \right) \beta = 0 \end{split} \tag{5}$$

Assuming that k_5 is negligible against 1, we can simplify the equation to

$$\lambda^{3} + (k_{4} - \alpha - \delta)\lambda^{2} + [\alpha\delta - \beta\gamma + k_{4}(\beta - \alpha - \delta)]\lambda + k_{4}\delta(\alpha - \beta) = 0$$
 (5 a)

Necessary for stability is that the coefficients of this equation are positive, i.e.,

$$\begin{cases} k_4 > \alpha + \delta \\ \alpha \delta - \beta \gamma > k_4 (\alpha + \delta - \beta) \\ \delta (\alpha - \beta) > 0 \end{cases}$$
 (6)

In our case $\alpha > 0$, $\beta = 0$ at the point M, and $\alpha < 0$, $\beta < 0$ at the point P, while always $\gamma > 0$, $\delta < 0$. The above conditions are not all fulfilled for the point M, and this is an unstable equilibrium point. Regarding the other point P, it is easily seen that all the above conditions are fulfilled when $\alpha < \beta$, or when

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$$\frac{\alpha}{-\beta} = \frac{\left(\frac{\partial f}{\partial x_1}\right)_{x_d = \text{const.}}}{-\left(\frac{\partial f}{\partial x_d}\right)_{x_l = \text{const.}}} = \left(\frac{dx_d}{dx_1}\right)_{f=0} < -1.$$

This means that the slope of the curve f = 0 in fig. 5 must be < -1 at the equilibrium point if this should be stable, or which is the same,

$$\left(\frac{\partial f}{\partial x_l}\right)_{\gamma_a = \text{const.}}$$
 must be < 0. One can possibly

think of curves which have negative slope and in such a case the pure presence of the sea would cause instability regardless of the characteristic rapidity of the adjustment between sea and atmosphere.

Furthermore, we cannot infer that the system is stable in the other normal case, since the above inequalities are only necessary conditions for stability. To get sufficient conditions, we have to add the inequality

$$\begin{vmatrix} k_4 - \alpha - \delta & k_4 \delta(\alpha - \beta) \\ I & \alpha \delta - \beta \gamma + k_4 (\beta - \alpha - \delta) \end{vmatrix} > 0$$
(condition of Hurwitz)

or developing

$$(k_4 - \alpha - \delta) \left[\alpha \delta - \beta \gamma + k_4 (\beta - \alpha - \delta) \right] > k_4 \delta (\alpha - \beta)$$
(7)

When $\alpha < \beta$, $\alpha < 0$, $\beta < 0$ this condition is certainly satisfied for sufficiently small (positive) or sufficiently large values of k_4 , but it will be violated within an intermediate interval, provided the two parameters

$$q = \frac{(\alpha + \delta)(\alpha + \delta - \beta)}{\alpha \delta - \beta \gamma}$$
$$r = \frac{\beta(\delta - \gamma)}{\alpha \delta - \beta \gamma}$$

take on values inside the ellipse $(q+\gamma)^2 = 4q$. To say more about this possibility will require numerical computations. Thus the sea can cause instability also for a normally shaped function $f(x_l, \gamma_a)$.

As to the complete trajectory field this will look much similar to the field shown in fig. 9 in the case where we have one stable and one unstable equilibrium point, except that the trajectories now run in the three-dimensional space. In the possible case where both the

equilibrium points become unstable, the picture will, however, change radically. Starting on a trajectory inside our region of existence $x_l > 0$, $x_d > 0$, $y_s > 0$, $x_l + x_d + y_s < a$, it cannot reach any of the boundaries provided the functions f and g are properly chosen, and it cannot end up at any equilibrium point. Three possibilities are then open. Either the trajectory approaches a certain limit curve, a limit-cycle, and we get ultimately a strictly periodic solution, or it approaches a thorus-shaped surface and we get a double-periodic solution, or finally it runs through the space in some ergodic manner in which case no periods can be found at all. See fig. 12.

One would guess, and it has also been confirmed by the numerical computations carried out on BESK, that the normal case is that of a limit-cycle.

It might finally be worth while to stress the difference between the ordinary linear oscillations around a stable equilibrium and the oscillations discussed here. In the former case, oscillations can be generated by external forces, but if they are not periodically sustained they will die out. In the latter case, once the system is disturbed slightly from its equilibrium, it runs into steady non-linear oscillations. To sustain the oscillations there must of course be a source of energy (in our system this source is represented by the sun, the radiation of which is required in all assimilation processes).

The essential result of this section is that the pure presence of the sea will cause self-sustained oscillations in our system, provided $\left(\frac{df}{dx}\right)$ is negative at the equilibrium

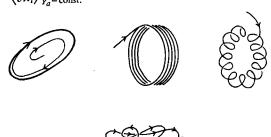


Fig. 12. Possible cases of limited trajectories around an unstable equilibrium point in a three-dimensional space. From left to right: limit-cycle (single-periodic solution) and two different "limit-thoruses" (double periodic solution). Below: "ergodic" motion.

point, i.e., assimilation decreases with increasing y_a . Such a state is, however, very unlikely. If this derivative is positive, such oscillations may also occur, but then only within a certain interval of k_a .

VII. Time delays in the biosphere

So far we have not complicated the system by assuming time delays. Naturally such a time delay would occur in forest vegetation. The trees build up their structural units of a quite large mass of assimilated CO2 which does not become available for decay until the trees die. It is thus not proper to assume that the rate of transition from living organic to dead organic matter is a function of the present amount of living matter; it would rather be a function of the amount of living matter some years earlier. This is somewhat equivalent to what might happen in animal populations. A high birth rate may increase the mass of the population, while the rate of death remains constant for a certain time, independent of the sudden increase in population. As HUTCHINSON (1949) has pointed out such time delays in biological systems may cause steady periodic fluctuations.

Also, there is a general experience in such engineering fields as electronics and servo regulation that time delays introduced in a feed-back system will often cause instability and appearance of self-sustained oscillations.

In our discussion of the delay, we have to split up the transfer function $f(x_l, y_a)$, since the delay should appear in the drain from living to dead organic matter but not in the assimilation.

Starting with the simplified case where the sea is left out of account, we have now the linearized equations

$$\frac{d\xi}{dt} = \alpha \cdot \xi + \beta \cdot \eta$$
$$\frac{d\eta}{dt} = \gamma \cdot \xi + \delta \cdot \eta$$

describing the behaviour of the system in the vicinity of the equilibrium point. The term $y\xi$ in the second equation represents the transfer from living to dead matter. Thus, rewriting the first equation in the form

$$\frac{d\xi}{dt} = (\alpha + \gamma)\xi + \beta\eta - \gamma\xi$$

the first two terms represent assimilation, and the last term represents the drain.

Introducing a time-delay in the transfer term $\gamma \xi$ means mathematically that ξ should be replaced by a new variable ξ^* which is coupled to ξ by some delay equation. The system is then

$$\frac{d\xi}{dt} = (\alpha + \gamma)\xi + \beta\eta - \gamma\xi^*$$

$$\frac{d\eta}{dt} = \gamma\xi^* + \delta\eta$$
(8)

The delay equation can be chosen in different ways. HUTCHINSON (1949) uses a delay equation of the form

$$\xi^{\bigstar}(t) = \xi(t-\tau)$$

i.e., ξ^* equals the value of ξ at a time τ ago. Such an equation is, however, not quite satisfactory in our case. The size of a plant at its death will not depend on the conditions of the environment at some specified earlier time but reflects the conditions prevailing over its whole life-time.

A more gradual response to outer changes of the delay variable would be obtained by use of the delay equation

$$\frac{d\xi^{\star}}{dt'} = \frac{1}{\tau} (\xi - \xi^{\star}) \tag{9}$$

expressing that the rate of change of the delay variable ξ^* is proportional to the deviation $\xi - \xi^*$. τ is the characteristic delay time. This equation can be considered as the linearized form near the equilibrium of the more general delay equation

$$\frac{dx_l^*}{dt} = h(x_l, x_l^*)$$

Theoretical reasons for using this type of delayfunction are found in the appendix.

Our system of differential equations (8) and (9) gives us now the frequency equation

$$\begin{vmatrix} \alpha + \gamma - \lambda & \beta & -\gamma \\ 0 & \delta - \lambda & \gamma \\ \frac{1}{\tau} & 0 & -\frac{1}{\tau} - \lambda \end{vmatrix} = 0$$

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or

$$\lambda^{3} + \left(\frac{1}{\tau} - \alpha - \gamma - \delta\right)\lambda^{2} + \left\{-\frac{1}{\tau}(\alpha + \delta) + (\alpha + \gamma)\delta\right\} \cdot \lambda + \frac{1}{\tau}(\alpha\delta - \beta\gamma) = 0$$
(10)

One sees that when $\tau \to 0$, this equation degenerates to the form (3), as is to be expected.

According to the above equation, the equilibrium point at $x_i = 0$ is still unstable, since $\alpha \delta - \beta \gamma$ is there < 0. Regarding the other equilibrium point, where $\alpha < 0$, $\delta < 0$, the coefficients of the equation are positive, for all values of τ , when $|\gamma| < |\alpha|$. When $|\gamma| > |\alpha|$ instability certainly occurs for sufficiently large τ -values. On the other hand, the Hurwitz condition

$$\begin{vmatrix} \frac{1}{\tau} - \alpha - \gamma - \delta & \frac{1}{\tau} (\alpha \delta - \beta \gamma) \\ 1 & -\frac{1}{\tau} (\alpha + \delta) + (\alpha + \gamma) \delta \end{vmatrix} > 0$$

OI

$$\left(\frac{1}{\tau}\right)^{2} - \left[\left(\alpha + \delta + \gamma\right) + \gamma \frac{\left(\beta + \delta\right)}{\alpha + \delta}\right] \frac{1}{\tau} + \frac{\delta(\alpha + \gamma)\left(\alpha + \delta + \gamma\right)}{\alpha + \delta} = 0$$
 (11)

shows that instability occurs for sufficiently large τ -values also when $|\gamma| < |\alpha|$.

Thus we arrive at the important result, that the system will always be unstable and run into self-sustained oscillations for a sufficiently large time-lag τ .

VIII. Numerical computations

In the numerical computations the basic system is assumed to have the specific form

$$\frac{dx_{l}}{dt} = k_{1}x_{l}\gamma_{a} - k_{2}x_{l}$$

$$\frac{dx_{d}}{dt} = k_{2}x_{l} - k_{3}x_{d}$$

$$\frac{dy_{s}}{dt} = k_{4}(\gamma_{a} - k_{5}\gamma_{s})$$

$$x_{l} + x_{d} + \gamma_{a} + \gamma_{s} = a$$
(12)

which is similar to a form given earlier, except that the term $k_1x_1y_a$ now represents the net assimilation. Taking from Section III the value 8 mg⁻² year⁻¹ for the rate of net assimilation and assuming that the values of x_1 , x_d , y_a and y_s tabulated there correspond to the equilibrium values x_{l_0} , x_{d_0} , y_{d_0} and y_{s_0} , one obtains

$$k_1 = 4.3 \cdot 10^{-5}$$
 mg⁻¹ cm² year⁻¹
 $k_2 = 2.0 \cdot 10^{-2}$ year⁻¹
 $k_3 = 1.6 \cdot 10^{-2}$ year⁻¹
 $k_5 = 1.8 \cdot 10^{-2}$

The corresponding values of the parameters α , β , γ and δ are

$$\alpha = k_1 \gamma_{a_0} - k_1 x_{l_0} - k_2 = -1.7 \cdot 10^{-2}$$

$$\beta = -k_1 x_{l_0} = -1.7 \cdot 10^{-2}$$

$$\gamma = k_2 = 2.0 \cdot 10^{-2}$$

$$\delta = -k_3 = -1.6 \cdot 10^{-2}$$

With these values it is found that the unequality (7) is fulfilled for all values of k_4 , and in fact one must change the values of the parameters very radically to violate it. Thus one may draw the conclusion that in this case the sea certainly cannot cause instability but merely will have a damping effect.

In the case of a time-lag in the biosphere the relevant condition for stability when the sea is left out is (11), which for the numerical values chosen will become

$$\left(\frac{1}{\tau}\right)^2 - 0.68 \cdot 10^{-2} \cdot \frac{1}{\tau} - 0.169 \cdot 10^{-4} > 0$$

and the critical τ -value above which instability occurs is about 100 years. Due to the presence of the sea, the critical value is decreased with a few decades, as can be judged from the complete equations. τ -values of that magnitude are likely to appear in the biosphere. Thus, one must conclude that instability and then also self-sustained oscillations very well might exist in the natural cycle.

The actual numerical computations of the time-development of the system on BESK were performed by a step-by-step integration of the system (12). In the case of a time-lag the term k_2x_1 was replaced by $k_2x_1^*$, and the delay equation

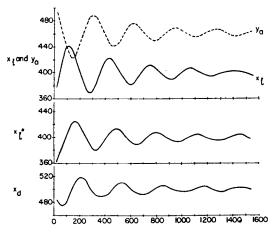


Fig. 13. Damped oscillations in the simplified model. Initial values $x_l = 360 \ x_l^{-1} = 360$, $x_d = 500$, $\gamma_a = 500$. $k_4 = 0$ (no sea), $\tau = 65$. The abscissa gives time in years.

$$\frac{dx_l^*}{dt} = \frac{1}{\tau} (x_l - x_l^*)$$

was added.

The results are shown in fig. 13—16. Fig. 13 shows a damped oscillation into the equili-

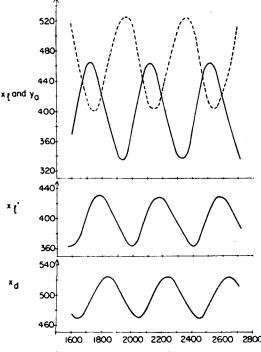


Fig. 14. The same case except that $\tau = 110$ years, giving self-sustained oscillations.

brium point in the case where the sea is left out of account. A time-lag $\tau = 65$ years is introduced, but it causes no instability. In fig. 14 is seen the corresponding solution when τ is increased to 110 years. In this case the system runs in to astate of self-sustained oscillations, with a period of about 400 years. Note the phase-difference between the curves for x_1 and y_a . In fig. 15 is seen the effect of the sea. Although a fairly "small" ocean is introduced ($k_5 = 0.184$), the effect is very marked; self-sustained oscillations appear already at $\tau = 70$ years and the period increases

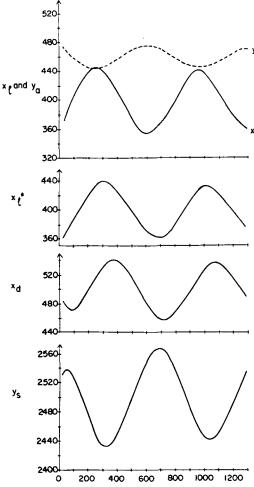


Fig. 15. The same case with part of the sea in exchange with the atmosphere. $k_5 = \frac{\gamma_a}{\gamma_5} = 0.184 \ (\gamma_5 = 2500, i.e.$ one tenth of the total volume). Self-sustained oscillations for $\tau = 70$ years.

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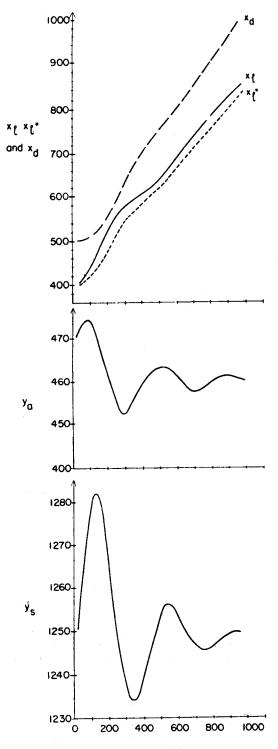
to about 700 years¹. Finally, fig. 16 shows the effect of an extra injection of carbon dioxide in the atmosphere at a rate corresponding roughly to the actual combustion of fossils. It is clearly demonstrated that most part of the added carbon dioxide is taken up by the biosphere, and that the atmospheric concentration is practically unchanged, except possibly during an initial transient period.

IX. General conclusions

Below is summarized the general conclusions that can be drawn from the previous discussion and the numerical computations:

- 1. The carbon cycle in the atmosphere-biosphere has two equilibrium points, one unstable point where no assimilating matter exists and another normal point, which is stable if there is no time-delay in the biosphere. Starting from the former point and introducing a small amount of assimilating matter, this will at first increase exponentially and then approach the other equilibrium point in an oscillatory manner.
- 2. The introduction of the sea does not radically change the previous picture. It cannot easily cause any self-sustained oscillations, but merely acts as a damping factor (a time-lag due to the deep-sea circulation can possibly cause such oscillations).
- 3. A time-delay of exponential type in the biosphere is reasonable. This will cause self-sustained oscillations in the system, if the time-lag τ is larger than a certain critical value, which is of the order of a hundred years. The period of the oscillations seems to be of order of several hundred years. It is possible that several oscillation states exist.
- 4. An injection of extra carbon dioxide in the atmosphere at a rate corresponding to the present rate of combustion of fossil carbon probably causes a marked increase of the carbon in the biosphere, while the atmospheric concentration is but little affected.

¹ In a paper by Fonselius and Koroleff in this issue of Tellus, all available data on CO₂ concentrations in the atmosphere from around 1850 up to now have been plotted in a diagram as function of time. Though the scatter in the values prior to 1900 is fairly large, it is rather tempting to interpret the secular variation in the concentration as an oscillation of the type shown here



The results quoted in (3) and (4) suggests that any observed increase of the carbon dioxide concentration in the atmosphere might represent part of a natural self-sustained oscillation rather than a response to an increased combustion of fossils.

Appendix

Derivation of the time delay equation

Let $F=F(t, \tau)$ be the distribution of assimilating mass, where t is time and τ is age of the mass. Then $F(t, \tau) d\tau$ is the mass of assimilating matter in the age interval between τ and $\tau + d\tau$.

The yearly assimilation is taken to be proportional to the concentration of carbon dioxide in the air, y_a , and to the amount of assimilating matter. Within an interval $d\tau$ we thus write,

net assimilation rate = $k_1 \gamma_a F d\tau$

where k_1 is regarded as independent of the

age τ.

The rate of transition of living mass to dead organic matter must also be proportional to $F d\tau$, but the proportionality constant depends also on τ . A simple and reasonable assumption is that the probability of death increases linearly with age so that rate of death = $\alpha \tau F d\tau$, where α is a constant

Naturally F must also change due to aging of the individuals and this contribution is simply

$$aging = -\frac{\partial F}{\partial \tau} d\tau$$

Then for the rate of change of F we have

$$\frac{\partial F}{\partial t} = k_1 \gamma_a F - \alpha \tau F - \frac{\partial F}{\partial \tau}$$

or

$$\frac{\partial}{\partial t}(\ln F) + \frac{\partial}{\partial \tau}(\ln F) = k_1 \gamma_a - \alpha \tau \qquad (1)$$

Fig. 16. Effect of an external source of carbon dioxide on the system, starting from equilibrium. $k_5 = 0.368$ ($\gamma_s = 1250$, i.e. 5 per cent of the total volume), $\tau = 50$, q = 1 (corresponding to the mean rate of combustion in the past). The abscissa gives time in years.

The characteristics of this partial differential equation are given by

$$dt = d\tau = \frac{d(\ln F)}{k_1 \gamma_a(t) - \alpha \tau}$$

and the general solution is found to be

$$F(t, \tau) = F(t, 0)e^{\left[\sum_{t=\tau}^{t} y_a(t)dt - \frac{\alpha \tau^2}{2} \right]}$$

F (t, 0) is the mass of successful seedlings and is assumed to have a small, constant value, F_0 . If γ_a is constant = $\overline{\gamma}_a$ (or varies but little) we have a normal distribution

$$F = F_0 e^{k_1 \overline{\gamma}_a \tau - \frac{\alpha \tau^2}{2}}$$

the maximum mass occurring at the age $\tau_m = \frac{k_1 \bar{\gamma}_a}{\alpha}$

For $\tau = 2 \tau_m$, $F = F_0$ again so that practically the whole mass is within the age limits $\tau = 0$ and $\tau = 2 \tau_m$.

By definition $x_l = \int_0^\infty F d\tau \approx \int_0^{2\tau_m} F d\tau$, where x_l is the total mass of assimilating material.

An integration of (1) gives, for $\overline{\gamma}_a = \gamma_a$,

$$\frac{d}{dt}\int\limits_{0}^{2\tau_{m}}Fd\tau=k_{1}\overline{\gamma}_{a}\int\limits_{0}^{2\tau_{m}}Fd\tau-\int\limits_{0}^{2\tau_{m}}\alpha\tau Fd\tau-\int\limits_{0}^{2\tau_{m}}\frac{\partial F}{\partial\tau}\,d\tau$$

or using earlier definitions and neglecting F_0 .

$$\frac{dx_{l}}{dt} = k_{1}\overline{\gamma}_{a}x_{l} - \int_{0}^{2\tau_{m}} \alpha\tau F d\tau$$
 (2)

Introducing the notation x_i^c for the integral $\int_{0}^{2\tau_m} \alpha \tau F d\tau$ we have further:

$$\frac{dx_{l}'}{dt} = \frac{d}{dt} \int_{0}^{2\tau_{m}} \alpha \tau F d\tau = \int_{0}^{2\tau_{m}} \alpha \tau \frac{dF}{dt} d\tau =$$

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$$\begin{split} &=k_1\overline{\gamma}_a\int\limits_0^{2\tau_m}\alpha\tau Fd\tau-\int\limits_0^{2\tau_m}\alpha^2\tau^2Fd\tau-\int\limits_0^{2\tau_m}\alpha\tau\frac{\partial F}{\partial\tau}d\tau=\\ &=k_1\overline{\gamma}_ax_i'-\int\limits_0^{2\tau_m}\alpha^2\tau^2Fd\tau-\int\limits_0^{2\tau_m}\alpha\tau\frac{\partial F}{\partial\tau}d\tau=\\ &=k_1\overline{\gamma}_ax_l'-\int\limits_0^{2\tau_m}\alpha^2\tau^2Fd\tau-[\alpha\tau F]_0^{2\tau_m}+\alpha\int\limits_0^{2\tau_m}Fd\tau=\\ &=k_1\overline{\gamma}_ax_l'+\alpha x_l-\int\limits_0^{2\tau_m}\alpha^2\tau^2Fd\tau \end{split}$$

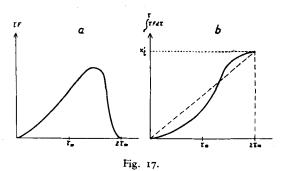
where (1) has been used.

The last integral can be evaluated, at least approximately, in the following way. By partial integration

$$\int_{0}^{2\tau_{m}} \alpha^{2} \tau^{2} F d\tau = \alpha^{2} \left[\tau \int_{0}^{\tau} \tau F d\tau \right]_{0}^{2\tau_{m}} - \alpha^{2} \int_{0}^{2\tau_{m}} \int_{0}^{\tau} F d\tau d\tau d\tau =$$

$$= 2\alpha \tau_{m} x_{l}^{\prime} - \alpha^{2} \int_{0}^{2\tau_{m}} \int_{0}^{\tau} \tau F d\tau d\tau d\tau \qquad (6)$$

As τF will give a distribution of the type shown in fig. 17 a, the integral $\int_{0}^{\tau} \tau F d\tau$ must look like the full darwn curve in fig. 17 b. The ntegral $\int_{0}^{2\tau_{m}} \tau \tau F d\tau$ d τ is then the area of the portion below the full drawn line and the τ -axis, between $\tau = 0$ and $\tau = 2\tau_{m}$. The simplest approximation which can be made is to replaze this by the triangular area indicated in the figure.



or

Then apparently the integral becomes $\tau_m x_l'$. However, some better approximation can be made by multiplying this expression by a constant B, which may be around unity. Then

$$\int\limits_{0}^{2\tau_{m}} \alpha^{2} \tau^{2} F d\tau \approx 2\alpha \tau_{m} x_{l}' - B\alpha \tau_{m} x_{l}'$$

and

$$\frac{dx'_l}{dt} = k_1 \gamma_a x'_l + \alpha x_l - 2\alpha \tau_m x'_l + B\alpha \tau_m x'_l =$$

$$= \alpha x_l - (\mathbf{I} - B) \alpha \tau_m x'_l$$

where the relation $k_1 \overline{\gamma}_a = \alpha \tau_m$ has been used. Introducing the new variable

$$x_l^* = (\mathbf{I} - B)\tau_m x_l'$$

and the characteristic time

$$\tau = \frac{\mathrm{I}}{\alpha(\mathrm{I} - B)\tau_m}$$

one obtains finally the delay equation

$$\frac{dx_l^*}{dt} = \frac{1}{\tau} (x_l - x_l^*) \tag{3}$$

Also, introducing

$$k_2 = \frac{\mathrm{I}}{(\mathrm{I} - B)\tau_m}$$

eq. (2) becomes

$$\frac{dx_l}{dt} = k_1 \bar{\gamma}_a x_l' - k_2 x_l^* \tag{4}$$

(3) and (4) can be identified with the delay equation and assimilation equation used in the computations of Sect. VIII.

An estimate of the constant B is obtained from the equilibrium case. Then $\frac{dx_l}{dt} = \frac{dx_l^*}{dt} = 0$

and the above equations give directly $k_2 = k_1 \overline{\gamma}_a$ or

$$\mathbf{I} \sim B = \frac{\mathbf{I}}{k_1 \overline{\gamma}_a \tau_m}$$

It is seen that B < I at equilibrium, which can also be anticipated from the distribution in fig. I a. It is, however, likely to vary when x_l deviates from the equilibrium value. If the equilibrium value of B is very near unity the approximation made here may become critical but if it departs considerably from unity the approximation is not so bad.

It is seen that the actual equilibrium value of B is among other factors determined by the value of τ_m chosen. It may be of interest to discuss this relation somewhat more. If the net equilibrium assimilation is \overline{b} , then $k_1\overline{\gamma}_a\overline{x}_l = \overline{b}$

$$I - B = \frac{\overline{x}_l}{\overline{b}\tau_m}$$

Apparently, in order to have any sense

 $\frac{x_l}{\overline{b}\tau_m} < 1$

 $au_m > \frac{\overline{x}_l}{\overline{b}}$

It has previously been assumed that y_a takes on a constant value \overline{y}_a , while actually it varies. Although even a small variation of y_a is important for the whole dynamics of the cycle, one can expect, however, that the coupling of y_a to the delay equation is relatively unimportant. The fluctuations of y_a , which are generally modest, will change the delay time τ somewhat, but this cannot noticeably affect the dynamic behaviour of the system, apart from the case where the system is near to a state of neutral stability.

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