

# *Modelling the Circulation of Carbon in the World's Terrestrial Ecosystems<sup>1, 2</sup>*

WILLIAM R. EMANUEL, GEORG E. G. KILLOUGH,<sup>3</sup> and JERRY S. OLSON.

## ABSTRACT

A mathematical model for the circulation of carbon in the world terrestrial ecosystems is proposed. A five-compartment representation is developed which corresponds to the functional components studied by field ecologists. Rate coefficients for this linear dynamic model are calculated from estimates of the 1970 standing crops and compartment exchanges of carbon. The model is analyzed in terms of response to a unit impulse, thereby displaying a transient time distribution. The response to a hypothetical pulse input through gross primary production is also simulated, illustrating the efficiency of the terrestrial carbon system in transferring carbon into longer storage components. Finally, the concept of CO<sub>2</sub> fertilization is examined by allowing gross primary production to increase in response to higher atmospheric concentrations. Although the standing crop of carbon in photosynthesizing compartments is induced to grow from a hypothetical preindustrial level to a specified 1970 level, the accompanying increase in other compartments is not as large as obtained in earlier model formulations which incorporate an input from the atmosphere directly to compartments containing carbon in woody material or soil.

## 1. INTRODUCTION

The relatively large amounts of carbon associated with the world's forests attract attention to the terrestrial reservoir as a major component of the global carbon cycle. The world forests might even be managed to increase carbon storage (Whittaker and Likens, 1973; Olson, 1975; Baes *et al.*, 1977). Even larger quantities of carbon are stored for longer periods of time in the soil than in live components of the terrestrial system (Schlesinger, 1977). An assessment of the magnitudes of terrestrial carbon

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<sup>3</sup>Health and Safety Research Division, Oak Ridge National Laboratory.

pools and associated residence times is difficult because of the large variability in vegetation across the landscape. Impressed on this spatial heterogeneity is a continual, and in many instances quite significant, change in carbon cycling due to natural growth and succession. The impact of man's activities on the global terrestrial system, particularly through forest clearing, further confounds the issue (Bolin, 1977; Woodwell *et al.* 1978). When viewed in the context of the CO<sub>2</sub>/climate issue, the effects of climate modification on the distribution and productivity of vegetation must also be considered.

In terrestrial ecosystems, carbon is assimilated from the atmosphere by photosynthesis and returned by respiration and fire. For natural communities viewed over reasonably long periods of time, net primary production (gross primary production less plant respiration) is balanced by heterotrophic respiration (from fungi, bacteria, and animals) and fire so that no net accumulation of carbon occurs. However, any sort of perturbation such as a change in climate or land use will upset this equilibrium so that particular portions of the terrestrial landscape may act as either source or sink for carbon with respect to the atmosphere. The enhancement of primary production in response to increased availability of atmospheric CO<sub>2</sub> has been suggested as another mechanism for pulling the terrestrial biota out of equilibrium, leading to additional accumulation of carbon. An unresolved issue is whether such increases, presumably slight so far, and regrowth following earlier clearing, possibly large, can overshadow the releases of carbon from additional loss (e.g. by decrease of forest area and diminished amounts per unit area).

To develop an understanding of carbon cycling in the terrestrial biota at the global scale, data collected at a limited number of study sites are extrapolated or integrated to the global scale using estimates of the areal extent of each ecosystem type. Quantitative studies of carbon cycling in total ecosystems have really only been undertaken in recent years. The International Biological Program (IBP), begun in 1964, is the most comprehensive in terms of spanning the range of ecosystem types, but individual related programs such as the Hubbard Brook Ecosystem Study provide additional information.

Two major difficulties arise in attempting to use carbon cycling data from IBP-style studies to construct an accounting of carbon circulation in the global terrestrial system. In choosing sites for intensive measurement and study, ecologists are attracted in many cases to less disturbed areas. In this sense, the collection of carbon studies currently available in the ecological literature is a less than desirable representative of the entire landscape complex. This shortcoming can be overcome to some degree by including information on commercial forestry operations and agriculture. However, these data must be used cautiously as they do not represent the total ecosystem structure and may be oriented to unusually productive sites.

A greater difficulty is the current rather than historical nature of information on carbon cycling in the terrestrial biota. Inventories of terrestrial vegetation reflect current conditions. Estimates of the preindustrial distribution, frequently based on the concept of potential vegetation, are tenuous because they depend on judgements of

what existed widely over regions that have since had their patterns complicated by patchworks of clearing and disturbed regrowth, if not altered completely (Olson, 1974; Rodin *et al.*, 1975). It is desirable to initiate simulations of global carbon dynamics prior to the time when the fossil fuel CO<sub>2</sub> input to the atmosphere became significant, perhaps 1860. A totally satisfactory way of reconstructing the required past history of the terrestrial carbon pool awaits the further development of inferential approaches (e.g., Stuiver, 1978; Wagener, 1978; Wilson, 1978; Freyer, 1979).

The purpose of this paper is to present a preliminary compartment model for the circulation of carbon in the world's terrestrial ecosystems. Although carbon is aggregated geographically and across all ecosystem types into one set of compartments, the model presented here embraces greater functional detail than previous representations which divided only live and dead or rapid and slow components of carbon. Based on an updated estimate of the inventory of carbon in terrestrial systems, an initial set of rate coefficients for carbon exchange between reservoirs is calculated. The resulting mathematical model is very preliminary, yet it can be used to explore, through simulation experiments, the general dynamic properties of the terrestrial carbon system.

## 2. ESTIMATES OF TERRESTRIAL CARBON INVENTORY

Central to understanding the role of terrestrial ecosystems in the global carbon cycle is the estimation of the inventory of carbon in these systems and exchange fluxes with the atmosphere. Ideally, these estimates should correspond to conditions that existed prior to major human influence (Olson, 1974). Historical records might then be used to derive changes in this natural inventory. Unfortunately, the preindustrial distribution of vegetation can only be judged indirectly, leaving estimates of the current terrestrial carbon inventory as probably the most reliable.

Numerous investigators have approached this estimation problem through essentially two avenues. The first is to develop a potential or natural distribution of vegetation over the earth's landforms by associating vegetation types with environmental conditions such as climate and soil. Maps of natural vegetation developed by Kuchler (1979) are typical of this approach. This idea has been extended by Lieth (1975) using simulation models to relate environmental conditions and primary productivity of the world's terrestrial ecosystems. The basic shortcoming of this method is that the human influence on land use is not taken in account. Kuchler classifies the large portion of the United States east of the Mississippi River and north of Mississippi, Alabama, and Georgia almost uniformly as dominated by various broadleaf deciduous tree communities. In reality, a large part of this region is intensely cultivated. Many wooded areas are now dominated by coniferous tree species either as early stages in natural succession or in commercially managed stands. Although the distribution of natural vegetation provides significant insight, it leads to a carbon inventory which is biased, being too large.

The second approach to developing more realistic estimates of the current inven-

given by Bolin, 1975). Carbon is distributed over a set of well-mixed reservoirs or compartments connected by fluxes. An ordinary first order differential equation reflecting material balance is associated with each compartment. Functions expressing the dependency of each flux on compartment contents and physical variables such as temperature are substituted in these mass balance equations. The resulting system of differential equations forms a model for the dynamics of the carbon cycle which can be solved, usually by numerical methods, to simulate time courses of the carbon content of each compartment from specified initial levels.

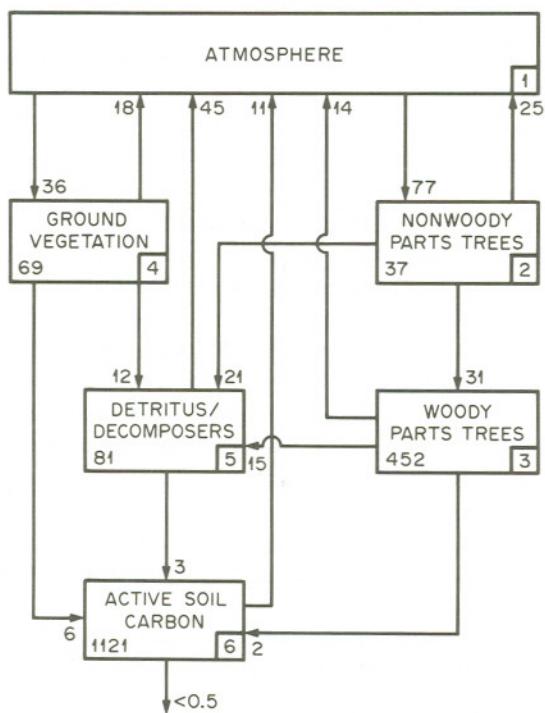


Figure 1: Compartment diagram for the circulation of carbon in the world's terrestrial ecosystems. Estimates of the 1970 standing crop of carbon (Gtons) for each compartment and annual average flows of carbon (Gtons/year) between compartments are indicated. The number of each compartment, corresponding to its variable assignment in the model equations, is boxed in each compartment. Total carbon in living material, 558 Gtons, is distributed over compartments 2, 3, and 4. Carbon in dead material, 1202 Gtons, is contained in compartments 5 and 6. The detritus/decomposers compartment corresponds to the surface layer of litter and its decomposers which receive input from the above-ground component of live material. The active soil carbon compartment is that part of soil carbon with turnover time much less than 1000 years. A small annual transfer is shown out of active soil carbon to longer turnover time soil components. This flux is neglected in formulating the model equations.

Several compartment model structures for representing terrestrial ecosystems in the global carbon cycle have been proposed. Generally, the terrestrial carbon reservoir has been divided into two compartments. This division has frequently been between live and dead (e.g., Eriksson and Welander, 1956; Bolin, 1970; Gowdy *et al.*, 1975). An alternative arrangement which allows greater flexibility in reflecting the range of characteristic response times of the terrestrial biota is the use of rapid and slow compartments corresponding to the mean residence times of carbon (e.g., Machta, 1971; Keeling, 1973, 1973; Bacastow and Keeling, 1973). Recent emphasis on the fluxes of CO<sub>2</sub> due to forest clearing has motivated the further division of these rapid and slow compartments geographically into northern and southern components (e.g., Chan *et al.*, 1979). These approaches share common difficulties. Any two-compartment system provides less resolution of response times than desired. More importantly, the compartments in these two-reservoir representations do not correspond directly with structural components normally considered by terrestrial ecologists; this makes comparison with data difficult. The compartment diagram in Fig. 1 which forms the basis for the model proposed here is an improvement in these respects.

Carbon in all live vegetation except trees is lumped into the single compartment that is labeled ground vegetation. Carbon in trees is divided into two compartments. The nonwoody compartment contains all photosynthesizing parts or foliage of trees plus flowers, fruits, and the transient growth of small roots; the woody pool contains carbon in branches, boles, and most roots. It is difficult to allocate the carbon in living parts of terrestrial ecosystems as summarized in Table 1 among these three live compartments. On the basis of currently available data, the total carbon in forest ecosystems is assigned to the trees reservoir; carbon in the remaining ecosystems is assigned to the ground vegetation pool. This assumption implies an approximate balance between the carbon in trees in nonforest ecosystems and that in ground vegetation in forest ecosystems. The amount of faster turnover carbon in ground vegetation in forest ecosystems may be underestimated, biasing the division of live carbon used here toward the tree pools.

Two compartments are used to lump carbon in dead parts of terrestrial ecosystems and their decomposers. The detritus/decomposers compartment represents the litter and its decomposers generally at the soil surface. This pool receives the direct input of carbon from death of live above-ground parts of vegetation. The active soil carbon pool is the carbon in soils and its decomposers which is still undergoing comparatively rapid decomposition. Carbon is transferred into this pool by death and initial decomposition of below-ground parts of vegetation and transport of decomposed material from the actively decaying litter layer. Respiration of organisms decomposing this active soil carbon pool give it a turnover time on the order of 100 years.

As previously indicated, a much less active soil carbon pool which is significant in the long-term storage of carbon is not included in the representation of terrestrial carbon circulation given here. As indicated by the output from the active soil carbon compartment (ignored in the model equations to follow), the input to this slowly decaying soil carbon pool composed mostly of deep peat, humus, and subfossil car-

bon is estimated to be less than 0.5 Gtons/year. The turnover time of the pool is on the order of 1000 years. While not necessarily important in studying changes in the atmospheric concentration of CO<sub>2</sub> over 200 year time intervals, more accurate assessment of the input to this long-term storage pool and modification due to man's activities is needed.

As illustrated in Fig. 1, the compartment representation for terrestrial circulation of carbon is viewed as being in equilibrium in 1970. Thus, fluxes in and out of each compartment and the total system of Fig. 1 are initially forced to balance. In some instances, this assumed equilibrium has been used to set the numerical value of certain fluxes, particularly those due to respiration. It is not likely that the terrestrial component of the carbon cycle is presently in equilibrium. The approach employed here is to use the assumption of 1970 equilibrium for model development and calibration. This equilibrium is then modified or unbalanced, based on alternative ideas of previous system status. This approach will likely stand until methods of inferring past histories of the carbon cycle are perfected.

The average fluxes of carbon between compartments given in Fig. 1 for 1970 are known with even less certainty than the estimates of standing crops. Again, data collected by many site-specific total ecosystem studies are averaged to yield the initial flux estimates used here. Particularly important are the data from 117 research sites accumulated in the IBP International Woodlands Data Set (DeAngelis *et al.*, in press). Estimates of gross primary production and total system respiration have been

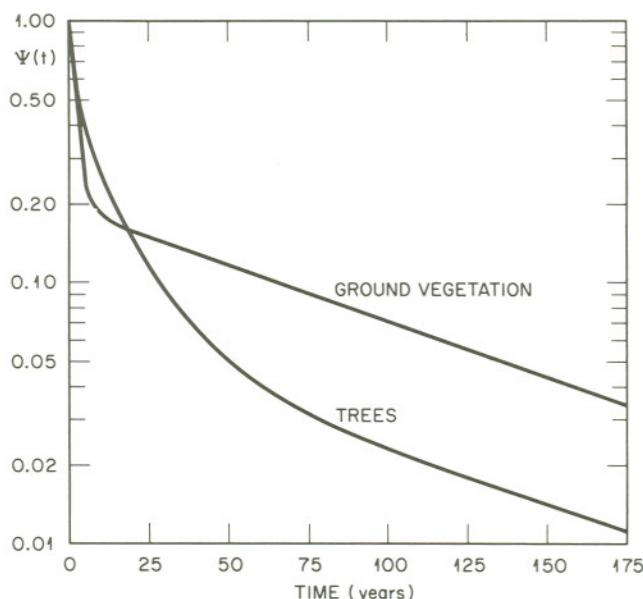


Figure 2. Impulse response of the five-compartment model for the circulation of carbon in terrestrial ecosystems. The response curves correspond to the fraction of an initial level of 1. Beyond 175 years, both curves continue to decrease linearly on this logarithmic scale.

retained from SCEP (1970), with autotrophic respiration by ground vegetation and nonwoody parts of trees adjusted to give net primary production equal to one-half of gross primary production. One-third of the net assimilated carbon by ground vegetation is assumed transferred directly to the active soil carbon pool by mortality of below-ground parts. The amount of carbon translocated from nonwoody to woody parts of trees is assumed balanced by respiration. A small transfer directly to the active soil carbon pool is due to death of below-ground parts of trees.

The total respiration of CO<sub>2</sub> from the ground surface has been measured for a number of terrestrial ecosystems. The appropriate component of dead material and its decomposers with which to associate this flux is not known. The ratio of this flux between detritus/decomposers and active soil carbon given in Fig. 1 is based on a balance with other fluxes for these compartments.

In developing the model equations corresponding to Fig. 1, a single first-order ordinary differential equation is used to express material balance for each compartment. The fluxes between compartments are assumed to be linearly proportional to the content of the donor compartment:

$$F_{ij} = k_{ij} N_i \quad (1)$$

where F<sub>ij</sub> is the flow of carbon from compartment i to compartment j (Gtons/year); N<sub>i</sub> is the standing crop of carbon in the donor compartment i (Gtons); and k<sub>ij</sub> is the corresponding rate coefficient (year<sup>-1</sup>). Utilizing the variables from Fig. 1, the model equations are

$$\frac{dN_2}{dt} = - 2.081 N_2 + F_{12}$$

$$\frac{dN_3}{dt} = 0.8378 N_2 - 0.0686 N_3$$

$$\frac{dN_4}{dt} = - 0.5217 N_{14} + F_{14}$$

$$\frac{dN_5}{dt} = 0.5676 N_2 + 0.0332 N_3 + 0.1739 N_4 - 0.5926 N_5$$

$$\frac{dN_6}{dt} = 4.425 \cdot 10^{-3} N_3 + 0.0870 N_4 + 0.0370 N_5 - 9.813 \cdot 10^{-3} N_6$$

where F<sub>12</sub> and F<sub>14</sub> are inputs of carbon to the terrestrial system corresponding to gross primary production.

Many of the transfers of carbon in Fig. 1 likely depend on the carbon contents of the compartments in a more complex way than captured by the linear assumption (1). Further, rates of carbon transfer are effected by environmental conditions such as temperature. Rodhe and Björkström (1979) have demonstrated that more complex functional relationships for carbon fluxes in compartment models of the global

carbon cycle can lead to significantly different system response. At present however, sufficient data are generally not available for calibration of more complex expressions for carbon fluxes. Until further refinement is possible, linear differential equations can be studied to gain preliminary understanding of the carbon cycle particularly with regard to the implications of different choices of compartmental structure or major changes in the relative magnitudes of fluxes between compartments.

#### 4. PRELIMINARY MODEL ANALYSES

The system of differential equations (2) forms a dynamic model for the circulation of carbon in terrestrial ecosystems which can be coupled to models for circulation in the atmosphere and oceans. The ultimate conclusions from adopting the view of the terrestrial carbon subsystem expressed by this model can only be evaluated in a total cycle context; however, it is instructive to carry out a preliminary analysis of this terrestrial module, decoupled from the remainder of the system, to clarify the general response characteristics of this part of the carbon cycle.

The linear structure of the model differential equations permits an analytical evaluation of the system dynamics by calculating the response to a unity initial condition in the system compartment which is excited by an input:

$$x(t) = e^{At} x_a(0), \quad (3)$$

where  $x$  is the vector of system variables;  $x_a$  is the corresponding vector of initial conditions, zero in all entries except 1 and 3 which are unity; and  $A$  is the matrix of rate coefficients extracted from (2). This response to a unit initial condition in a forced compartment is equivalent to the response of the system to an impulse. A single valued function of the system variables is considered as the output, in this case the sum of the material in each compartment:

$$\Psi(t) = \sum_{i=2}^6 N_i(t) \quad (4)$$

This type of analysis, i.e., calculation of  $e^{At}$ , is equivalent to the analysis of the transit time distribution function suggested by Bolin (1975). This impulse response as shown in Fig. 2 reflects the fraction of carbon remaining in the terrestrial system as a function of time. Note that the logarithm of this fraction continues to decrease linearly after 175 years.

The response characteristics of the five-compartment model of terrestrial carbon circulation are further elucidated by calculating the response to a hypothetical pulse in gross primary production. The system in steady state with a constant input is excited by a pulse of ten years duration and amplitude of 5 Gtons/year. The system response is shown in Fig. 3. The width of the response to the pulse broadens and the point of maximum amplitude is later for slower compartments further removed from the atmosphere. In Fig. 4, the total flux of carbon, above the steady-state level, into the woody parts of trees and active soil carbon compartments resulting from the

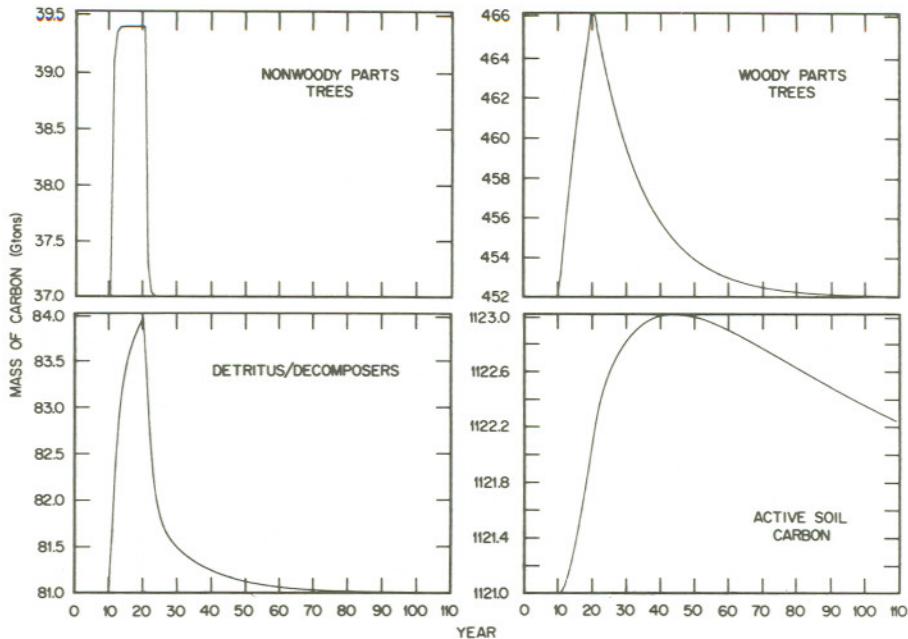


Figure 3: Response of terrestrial carbon circulation model to a hypothetical pulse in gross primary production by trees. The system is initially in steady state to constant inputs of 77 Gtons/year to nonwoody parts of trees and 36 Gtons/year to ground vegetation. The pulse is applied at 10 years with an amplitude of 5 Gtons/year and a duration of 10 years.

pulse in gross primary production by trees is plotted. Of the 50 Gtons of carbon placed in the system by the pulse input, 20.13 Gtons (40%) enters the woody compartment and 2.77 Gtons (5.5%) enters the active soil carbon compartment. The efficiency of the terrestrial carbon system in transferring material to longer turnover-time reservoirs is reflected by this result.

Several investigators have suggested that the assimilation of carbon dioxide by terrestrial plants might be enhanced by increases in the concentration of CO<sub>2</sub> in the atmosphere. Limited experimental evidence supporting this CO<sub>2</sub> fertilization hypothesis has been obtained from greenhouse studies. Considerable controversy is centered on the degree to which CO<sub>2</sub> might be limiting in natural ecosystems. In many systems, major nutrients such as nitrogen or phosphorus or soil moisture limit the rate of gross primary production and therefore the uptake of CO<sub>2</sub> from the atmosphere. For many individual plants the availability of light is also an important limiting factor. At the global scale, the degree to which CO<sub>2</sub> fertilization might be significant is not known. A review of this issue is given by Goudriaan and Ajtay (1979).

Noting this uncertainty, it is instructive to incorporate a function for dependence of gross primary production on atmospheric CO<sub>2</sub> in models for terrestrial carbon circulation and evaluate the effects on system dynamics. The function suggested by Bacastow and Keeling (1973, 1977) has been substituted for the gross primary pro-

duction of compartments 2 (nonwoody parts of trees) and 4 (ground vegetation) in Fig. 1:

$$F_{12} = k_{12} \cdot (1 + \beta_{12} \cdot \ln(N_1/N_{10})) \cdot N_2 \quad (5)$$

$$F_{14} = k_{14} \cdot (1 + \beta_{14} \cdot \ln(N_1/N_{10})) \cdot N_4 \quad (6)$$

The compartment system of Fig. 1 allows a conceptually different approach to incorporating CO<sub>2</sub> fertilization in the model. The flux of carbon into the photosynthesizing compartments increases logarithmically, with increases in atmospheric CO<sub>2</sub> forcing these pools to grow. Remaining components of the terrestrial system then respond based on the linear system interconnections specified by equations (2).

The parameters in equations (5) and (6) have been chosen in the following way. Choosing t = 0 to correspond to a preindustrial steady state at year 1860, calculate

$$k_{12} = \frac{F_{12}(t=0)}{N_2(t=0)} \quad (7)$$

$$k_{14} = \frac{F_{14}(t=0)}{N_4(t=0)} \quad (8)$$

The parameters  $\beta_{12}$  and  $\beta_{14}$  are then chosen through simulation experiments or an optimal parameter estimation scheme so that the pool sizes  $N_2$  and  $N_4$  correspond to the 1970 values from Fig. 1 or Table 1.

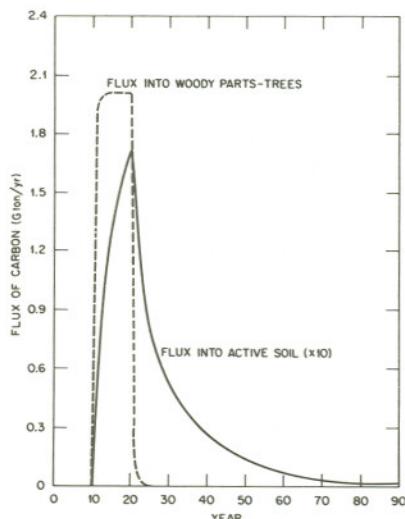


Figure 4: Inputs of carbon to woody parts of trees and active soil compartments in response to a pulse in gross primary production by trees beginning in year 10 of the simulation with amplitude of 5 Gtons/year and a duration of 10 years. The system is initially in steady state. The steady-state fluxes have been subtracted so that only levels associated with the pulse input are reflected. The total amount of carbon (area under curve) associated with these fluxes is 20.13 Gtons for woody parts and 2.77 Gtons for active soil.

The amount and distribution of carbon in terrestrial ecosystems in 1860 is not known. In their model simulations, Bacastow and Keeling (1973) assume the preindustrial mass of carbon in the terrestrial system to be 1635 Gtons. Actually, the 1860 terrestrial carbon pool was probably larger than at present, having been reduced by changes in land use. However, the response of models of terrestrial carbon circulation to CO<sub>2</sub> fertilization can still be investigated by choosing an arbitrary initial condition to be altered as additional data become available. To allow comparison of model responses, 1635 Gtons is assumed here and distributed among the terrestrial compartments in the same ratio as the 1970 levels of Fig. 1. Maintaining the same ratios among compartment contents implies that increases in atmospheric CO<sub>2</sub> serve only to enhance gross primary production without otherwise changing the structure of the system. Initial conditions for the terrestrial compartments are assumed to be:

$$\begin{aligned} N_2(t = 0) &= 34.37 \text{ Gt} \\ N_3(t = 0) &= 420.0 \text{ Gt} \\ N_4(t = 0) &= 64.10 \text{ Gt} \\ N_5(t = 0) &= 75.25 \text{ Gt} \\ N_6(t = 0) &= 1041 \text{ Gt} \end{aligned} \quad (9)$$

To maintain these levels as an 1860 steady state, constant forcing functions corresponding to gross primary production by trees (F<sub>12</sub>) and ground vegetation (F<sub>14</sub>) of

$$\begin{aligned} F_{12}(t = 0) &= 71.53 \text{ Gt/yr} \\ F_{14}(t = 0) &= 33.44 \text{ Gt/yr} \end{aligned} \quad (10)$$

are required. From equations (7) and (8),

$$k_{12} = 2.081 \text{ yr}^{-1} \text{ and } k_{14} = 0.5217 \text{ yr}^{-1} \quad (11)$$

In testing the biota growth formulation with the terrestrial carbon circulation model proposed here, the level of carbon in the atmosphere is assumed to be given by the function

$$N_1(t) = N_1(t = 0) + \rho \cdot (t - 1860)^{\sigma} \quad (12)$$

$$\rho = [N_1(1958.5) - N_1(1860)] \cdot [1958.5 - 1860]^{-\sigma} \quad (13)$$

$$\sigma = \frac{a_1(1958.5 - 1860)}{N_1(1958.5) - N_1(1860)} \quad (14)$$

for the years 1860 through 1958.5. The parameter a<sub>1</sub> is the first derivative of the function (12) at t = 1958.5. Over the interval 1958.5 to 1975.5 the annual average measurements of CO<sub>2</sub> concentration at Mauna Loa, Hawaii (Keeling *et al.*, 1976) are converted to mass of carbon in the atmosphere and interpolated using cubic splines. The value of a<sub>1</sub> is set equal to the first derivative of the interpolating spline in 1958.5. The initial level of carbon in the atmosphere is assumed to be 607.48 Gtons corresponding to a CO<sub>2</sub> concentration of 285 ppm by volume. Use of the function (12) specifies a smooth monotonic increase in atmospheric carbon from this assumed initial condition to the beginning of the Mauna Loa record.

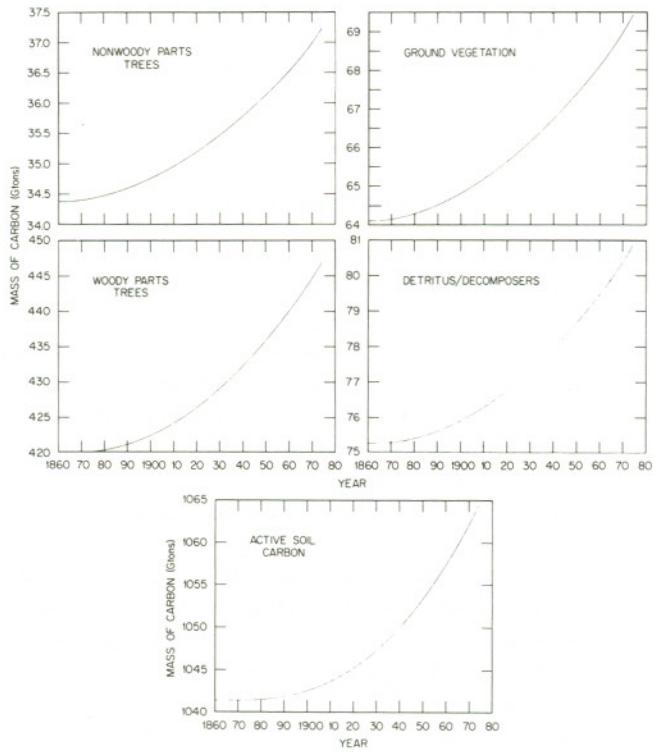


Figure 5: Response of the terrestrial carbon circulation model with gross primary production functionally dependent on the concentration of  $\text{CO}_2$  in the atmosphere. The system is arbitrarily assumed to contain a total of 1635 Gtons. The atmospheric concentration of  $\text{CO}_2$  is specified by measurements from 1958 to 1974 extrapolated back to an 1860 initial condition of 285 ppm by a smooth function. Parameters in the functions for gross primary production are adjusted so that photosynthesizing compartments increase to 1970 levels as given in Fig. 1.

Estimated by repeated simulation experiments, values of the biota growth factors of

$$\begin{aligned}\beta_{12} &= 0.00525 \\ \beta_{14} &= 0.0209\end{aligned}\tag{15}$$

cause a transition from the 1860 levels (9) to 1970 values, corresponding to Fig. 1 for compartments 2 and 4. The response of the system is shown in Fig. 5.

The 1970 levels of the nonphotosynthesizing compartments given by this simulation are

$$\begin{aligned}N_3(1970) &= 444.65 \text{ Gtons} \\ N_5(1970) &= 80.42 \text{ Gtons} \\ N_6(1970) &= 1062.19 \text{ Gtons}\end{aligned}\tag{16}$$

and the total mass of carbon in the terrestrial system in 1970 is 1693.27. This level is considerably lower than the total of Table 1, indicating that with the growth of photosynthesizing components generated, the transfer of carbon to other compartments is not sufficient to reach the 1970 level.

## 5. DISCUSSION AND SUMMARY

The five-compartment model for the circulation of carbon in terrestrial ecosystems presented here is based on a model structure which parallels the components of these systems (as studied by field ecologists) more closely than many earlier models. Simulation experiments using this model can therefore be compared more readily with field data. Perhaps more important in resolving the uncertainty about future increases in atmospheric CO<sub>2</sub> concentration resulting from man's continued use of fossil fuels is the more detailed treatment of the residence times in various pools of the terrestrial carbon circulation system.

It is important to establish the propensity of the terrestrial carbon system to act as a sink for carbon from the atmosphere independent of whatever carbon may be released to the atmosphere as a result of forest clearing and associated burning. Turnover times for the compartments in the terrestrial system range from approximately 5 years for photosynthesizing compartments to 15 years for woody parts of trees and 100 years for active soil carbon. Storage for periods of time sufficiently long to affect the rate of increase in atmospheric CO<sub>2</sub> due to fossil fuel combustion is to a large extent dependent on the terrestrial system's ability to transfer carbon to one of the latter two longer turnover-time compartments or ultimately to the very slow responding components of soil carbon not included in the present analysis. The system impulse response, Fig. 2, indicates that this efficiency of long term storage is not too great; 80% of the initial carbon content is released in 15 years. It is interesting to note however, that a larger fraction of carbon assimilated by ground vegetation is retained in the slowest responding component of the system than that assimilated by trees due to the relatively large direct transfer from below-ground parts of ground vegetation to active soil carbon.

Analysis of the response of the model of the terrestrial carbon system to a pulse demonstrates the isolation of the active soil carbon pool from changes in atmospheric carbon levels due to losses, mainly respiration, by intermediate compartments. This relatively large slow turnover reservoir has the potential for significant storage of the CO<sub>2</sub> released by fossil fuel combustion; however, the efficiency of transfer through the live compartments and detritus pool is not great. Of 50 Gtons of carbon put in the system by the pulse applied to the nonwoody parts of trees compartment, 2.77 Gtons enters the active soil carbon pool. It is interesting to note that the maximum in active soil carbon is delayed over that in tree nonwoody parts by only 27 years.

The enhancement of primary production by the biota in response to increased concentration of CO<sub>2</sub> in the atmosphere continues to be appealing from a modeling

point of view. Bacastow and Keeling (1979) indicate that our 1970 estimate of the active terrestrial carbon pool, 1760 Gtons, might be an upper limit on that pool at present. Beginning with an 1860 total carbon pool of 1635 Gtons and increasing the photosynthesizing compartments at a rate which carries them to the 1970 estimated levels does not increase the total terrestrial pool to 1760 Gtons but rather to a substantially lower level, 1693 Gtons. This is again a reflection of the efficiency of the terrestrial carbon system in transferring carbon from the photosynthesizing components to the longer-storage compartments.

It is assumed in the model presented here that CO<sub>2</sub> fertilization simply increases gross primary production and therefore the content of the photosynthesizing compartments of the system. Increase in other compartments is then induced by the transfer of carbon from these source pools. The rate coefficients or efficiencies of transfer are assumed to be unaltered. To support a larger increase in the terrestrial carbon pool than given by these simulations, at least some transfer rates must be changed. The extreme might be to assume that the amount of carbon in photosynthetic material remains constant and that CO<sub>2</sub> fertilization serves to increase the efficiency of transfer to other terrestrial components.

Three major topics for further study using this model are suggested. The first is to explicitly incorporate fluxes of carbon due to forest-clearing. The potential approaches to modeling these transfers are discussed in detail by Moore *et al.* (this volume); the emphasis here is on the natural terrestrial carbon circulation. Second, as pointed out by Schlesinger (this volume), the age distribution of dead carbon is more complex than is captured by the two compartments of this model. In reality, decaying material passes through a number of stages; i.e., there is a fair range of turnover times associated with this component. Third, a number of simulation experiments should be run to test the potential ability of this system to store carbon.

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