of plate motion, as suggested by Stewart and by Ninkovich and Donn, but rather of the diagenesis of ash layers.

Major, apparently global volcanic episodes occurred at least twice in the last 20×10^6 years. Yet, only one major glacial epoch (the Pleistocene) has occurred. Therefore, even though glaciation coincided with an increase in Quaternary volcanism, the increased volcanism itself may not have been the primary cause of global cooling.

References and Notes

1. J. P. Kennett and R. C. Thunell, *Science* **187**, 497 (1975).
2. R. J. Stewart, *Nature (London)* **258**, 505 (1975).
3. D. Ninkovich and W. L. Donn, *Science* **194**, 899 (1976).
4. J. R. Bray, *Nature (London)* **252**, 679 (1974); *ibid*. **260**, 414 (1976).
5. K. F. Scheidegger and L. D. Kulm, *Geol. Soc. Am. Bull.* **86**, 1407 (1975).
6. D. Ninkovich, B. C. Heezen, J. R. Conolly, L. H. Burckle, *Deep-Sea Res.* **11**, 605 (1964); D. Ninkovich, N. Opdyke, B. C. Heezen, J. H. Foster, *Earth Planet. Sci. Lett.* **1**, 476 (1966).
7. J. R. Hein, D. W. Scholl, C. E. Gutmacher, in *Proceedings International Clay Conference*, S. W. Bailey, Ed. (Applied Publishing, Wilmette, Ill., 1976), p. 71.
8. J. R. Hein and D. W. Scholl, *Geol. Soc. Am. Bull.*, in press.
9. Time boundaries are based on diatom zones, and ages of sections lacking microfossils are determined by extrapolation of sedimentation rates, most commonly 84 meters per 10^6 years. This technique provides a first-order approximation only, and the inherent limitations should be kept in mind. Time boundaries could be refined with paleomagnetic and radiometric dates.
10. R. R. Coats, *U.S. Geol. Surv. Bull. 974-B* (1950), p. 35; in *The Crust of the Pacific Basin*, G. A. MacDonald and H. Kuno, Eds. (American Geophysical Union Monograph 6, National Academy of Sciences–National Research Council Publication 1035, National Academy of Sciences, Washington, D.C., 1962), p. 92.
11. D. W. Scholl, M. S. Marlow, N. S. MacLeod, E. C. Buffington, *Geol. Soc. Am. Bull.* **87**, 547 (1976).
12. A. R. McBirney, J. F. Sutter, H. R. Naslund, K. G. Sutton, C. M. White, *Geology* **2**, 585 (1974).
13. R. L. Armstrong, *ibid.* **3**, 356 (1975).
14. E. H. McKee, D. L. Swanson, T. L. Wright, *Geol. Soc. Am. Abstracts with Programs* **9** (No. 4), 463 (1977).
15. E. H. McKee, D. C. Noble, M. L. Silberman, *Earth Planet. Sci. Lett.* **8**, 93 (1970); D. C. Noble, *ibid.* **17**, 142 (1972); P. W. Lipman, H. J. Prostka, R. L. Christiansen, *Philos. Trans. R. Soc. London Ser. A* **271**, 217 (1972); R. L. Christiansen and P. W. Lipman, *ibid.*, p. 249; J. W. Hawkins and D. L. Hawkins, *Geol. Soc. Am. Abstracts with Programs* **9** (No. 4), 432 (1977).
16. D. C. Noble, E. H. McKee, E. Farrar, U. Petersen, *Earth Planet. Sci. Lett* **21**, 213 (1974).
17. E. D. Jackson, H. R. Shaw, K. E. Bargar, *ibid.* **26**, 145 (1975).
18. T. L. Vallier, *Initial Rep. Deep Sea Drill. Proj.* **25**, 515 (1974).
19. J. R. Hein, *Nature (London)* **241**, 40 (1973); *J. Geophys. Res.* **78**, 7752 (1973); T. Atwater and P. Molnar, in *Conference on Tectonic Problems of the San Andreas Fault System*, R. L. Kovach and A. Nur, Eds. (Proceedings of Stanford University Publications in the Geological Sciences 13, Stanford University, Palo Alto, Calif., 1973), p. 136.
20. D. A. Clague and R. D. Jarrard, *Geol. Soc. Am. Bull.* **84**, 1135 (1973).
21. P. R. Vogt, *Nature (London)* **240**, 338 (1972).
22. C. Emiliani and J. Geiss, *Geol. Rundsch.* **46/2**, 576 (1958); N. Calder, *Nature (London)* **252**, 216 (1974); J. Chappel, *ibid.*, p. 199; C. G. A. Harrison and J. M. Prospero, *ibid.* **250**, 563 (1974); P. Thompson, H. P. Schwarcz, D. C. Ford, *Science* **184**, 893 (1974); J. Chappel, *Earth Planet. Sci. Lett.* **26**, 370 (1975); J. C. Duplessy, L. Chenouard, F. Vila, *Science* **188**, 1208 (1975); G. E. Williams, *Earth Planet. Sci. Lett.* **26**, 361 (1975); J. D. Hays, J. Imbrie, N. J. Shackleton, *Science* **194**, 1121 (1976); D. W. Parkin, *Nature (London)* **260**, 28 (1976).
23. We thank R. J. Stewart and J. A. Barron for helpful discussions and C. E. Gutmacher, M. G. Jones, and C. Price for technical assistance. T. L. Vallier, E. D. Jackson, and E. H. McKee provided critical reviews. We acknowledge assistance from the staff of the National Science Foundation's Deep Sea Drilling Project and the scientists and crew of the *Glomar Challenger*.

The Biota and the World Carbon Budget

The terrestrial biomass appears to be a net source of carbon dioxide for the atmosphere.

G. M. Woodwell, R. H. Whittaker, W. A. Reiners,
G. E. Likens, C. C. Delwiche, D. B. Botkin

Over the past 7 years several reviews of the world carbon budget have confirmed that there is an annual increase in the carbon dioxide content of air that is worldwide and is almost certainly man-caused (*1-7*). The source of the carbon that is accumulating in the atmosphere has been commonly assumed to be the combustion of fossil fuels. Because the amount of CO_2 accumulating in the atmosphere is less than half the total released from fossil fuels, other sinks for CO_2 have been sought. The major sink is the oceans, but mixing rates appear to be too low for the oceans to accommodate all the CO_2 that is thought to be released in excess of that accumulating in the atmosphere. The question of whether the terrestrial biota could be another sink was raised in 1970 (*1*), and the assumption was made that the biota might be a sink, especially in view of the stimulation of photosynthesis under greenhouse conditions by enhanced concentrations of CO_2. More recently the assumption that increased CO_2 in air stimulates photosynthesis worldwide has been questioned (*8-11*). So has the assumption that the biota is a net global sink for CO_2 (*3*). A series of current appraisals suggests that, quite contrary to the previous estimates, the biota is probably an additional source of CO_2 (*12-16*).

In this article we review briefly current knowledge of the world carbon budget with special emphasis on the question of whether the biota is now a source or a sink for CO_2. The analysis shows through convergent lines of evidence that the biota is not a sink and may be a source of CO_2 as large as or larger than the fossil fuel source. The issue is important because of the potential that changes in the CO_2 content of air have for changing climate worldwide (*2, 10*).

Two aspects of the world carbon budget are conspicuous at the moment because they are easily measured: the annual increase in the concentration of CO_2 in air, and the winter-summer oscillation in CO_2 concentration that is apparent in the middle latitudes, especially in the Northern Hemisphere. These variations trace the interplay among physical, chemical, and biotic factors of atmosphere, oceans, and the biota as affected by man. Although the world circulation of carbon is not well enough known to allow precise interpretation of past interactions, and predictions are still more tenuous, various analyses suggest that human activities in the near future could release large additional amounts of CO_2 into the atmosphere with results that are substantially unpredictable.

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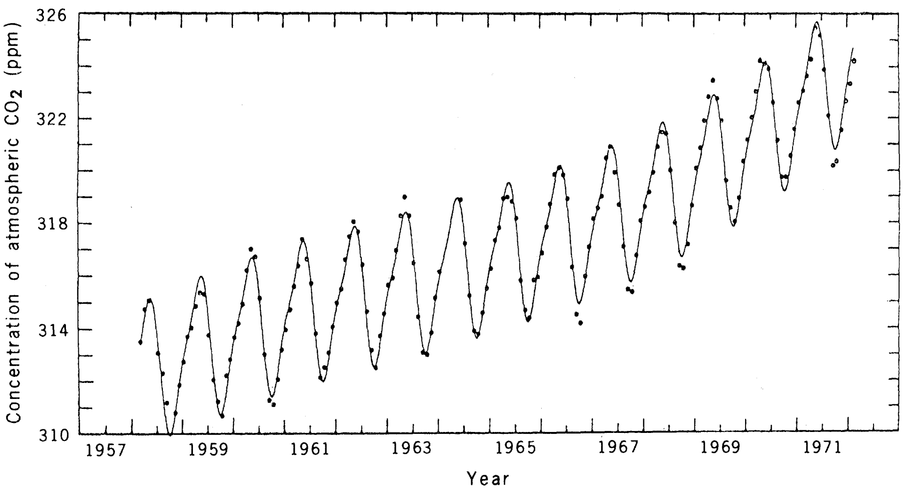

Fig. 1. Long-term variations in the CO_2 content of air at Mauna Loa Observatory. [From Eckdahl and Keeling (*18*)]

The data on the CO_2 content of air show an increase that has ranged in different observatories and at different times between about 0.5 and 1.5 parts per million (ppm) per year over more than 15 years (*17-19*). The upward trend has been assumed to be caused by the release of carbon from fossil fuels (*20*). At the same time an annual oscillation in the CO_2 content of air is apparent with a peak concentration at Mauna Loa in mid-April about 5 ppm higher than the minimum that occurs in late summer (Fig. 1). The oscillation is reduced in amplitude at higher elevations (*21*), is in excess of 15 ppm near sea level at Brookhaven, New York (*19*), diminishes toward the tropics, and is reversed to follow the seasons of the Southern Hemisphere (*22*). We infer from this pattern that the oscillation is related to the annual course of photosynthesis and gives powerful evidence that biotic exchanges are important in affecting the CO_2 content of the atmosphere.

World Carbon Budget

The pools of carbon that are interacting in the short term of a few years are similar in size and are connected by flows that are significant fractions of the pools. The sizes of the pools (Fig. 2) are subject to considerable uncertainty. For the carbon held within plant communities we have used estimates by Whittaker and Likens (*23, 24*) who considered their appraisal appropriate for the world of the 1950's.

The fluxes that connect these pools are a continuous exchange with the biota, a constant exchange between the atmosphere and the oceans, and the emission of CO_2 through combustion of fossil fuels. The fact that the terrestrial biota and humus together contain a pool of carbon that is probably between two and three times the total in the atmosphere means that any appreciable change in the biota has the potential to cause a short-term change in the CO_2 content of air, a relationship that seems to be substantiated by the seasonal oscillations seen in the CO_2 data from Mauna Loa. This flux could go in either direction—into storage in the biota and in humus, or out of storage into the atmosphere. The question has been considered in most models in recent years with a common assumption that the biota is probably a sink for the excess of carbon released in combustion of fossil fuels above the residue that accumulates in the atmosphere and appears not to be absorbed into the oceans (*25-27*). The assumption has remained a part of current global models. It seems to be incorrect. As suggested by Hutchinson (*13*) in 1954 the biota appears to be a net source of CO_2 for the atmosphere. Because of the paucity and uncertainty of data the actual rate of release is elusive; under extreme conditions it could be as high as 18×10^{15} grams of carbon per year, or more than three times the annual release of carbon through combustion of fossil fuels, currently estimated as about 5×10^{15} g (*28*).

The total amount of carbon held within the living biota in the 1950's was about 830×10^{15} g; more than 90 percent was in the standing crop of plants in forests and woodlands (Table 1). Of the total within forests and woodlands, 461×10^{15} g, or about 60 percent, was in tropical forests. The carbon held within terrestrial humus has been estimated recently as 1000 to 3000×10^{15} g, or one to four times the quantity in the living biota (*4, 29*). The distribution of carbon in the biota is skewed toward the tropics by the overwhelming mass of the tropical forests; the humus is more abundant in the temperate and boreal zones where lower temperatures retard decay. The balance between inputs and outputs of carbon in these two large pools will determine whether there is a net release of carbon into the atmosphere from organic carbon pools at any time.

Changes in the Biotic Carbon Pool: Estimates Based on Harvests

Over the last millennium the shift in the size of the carbon pool within the biota seems clear: forests have been reduced appreciably as human population has increased. Darby (*30*) estimated that the forests of Western Europe were reduced from more than 90 percent of the land area to between 18 and 23 percent in the thousand years following A.D. 900. A parallel reduction, documented in part by Eckholm (*31*), occurred earlier in segments of the Mediterranean Basin, the Levant, and Asia. These changes released significant quantities of carbon, perhaps as much as 25 percent of what is currently held within the atmosphere. The question is better restricted to the past 100 years. What has happened to the standing crop of forests and humus in the world over the last 100 years, and especially since 1958 when the CO_2 record at Mauna Loa was started?

Using data from the Food and Agriculture Organization (FAO) and other sources, Bolin (*14*) recently calculated the net release of CO_2 from the harvest of forests globally as 1.0×10^{15} g of carbon per year. The estimate appears to have been biased toward the low side (*32*).

The question of harvesting and clearing is especially important for the tropical forests of South America because the Amazon Basin contains the most extensive primary rain forest remaining in the world. Detailed data on the extent of harvest of this forest are limited. A recent study by Veillon (*33*) of forest clearing in Western Llanos, Venezuela, showed a 32.5 percent reduction in forest area during the period 1950 to 1975, corresponding to an average rate of deforestation of about 1.3 percent per year. According to Hamilton (*34*, p. 4) "one can presume that, with the exception of the Sierra de Perija, changes are taking place at somewhat similar rates in general north of the Orinoco." Hamilton cited an FAO draft report that "suggests an *estimate* of moist forest cleared per year at . . . 0.6 to 1.5 percent of the still existing area" (*34*, p. 4). Other studies support the trend (*35*). Adams *et al.* (*15*) cited data for two Brazilian states. São Paulo (total area, 250,000 square kilometers) was 60 percent forested in 1910; by 1950 the area forested was 20 percent. In Paraná between 1953 and 1963 the forested area of 65,000 km^2 decreased at the rate of 3 percent per year. The development of the Trans-Amazonian Highway appears to have speeded the harvest in the Amazon (*36*). So has the growth of population with its demand for firewood, according to Adams *et al.* (*15*) and Eckholm (*31*).

The remaining primary forests of the temperate and boreal zones are less important in the world carbon budget, yet they are subject to a parallel pressure for harvest. If a rate of clearing of 1 to 2 percent per year were applied to the forests of the earth, which we take to have a total plant mass of 743×10^{15} g of carbon (Table 1) (*24*), and if two-thirds of the biomass were released as CO_2 with the remainder stored, the amount of carbon released annually would be 5 to 10×10^{15} g—one to two times the amount currently released from fossil fuels. If we consider only the tropical forests, the amount released would be about 3 to 6×10^{15} g of carbon annually.

In addition to this release from direct harvest of forests there is further release from humus that is triggered by deforestation. Although humus accumulation in some tropical forests is small, extensive areas of the tropics have podzols and histosols with appreciable humus layers. The transformation of forests and wetlands to agriculture also leads to a loss of humus through decay (*37, 38*). To the extent that forests are being reduced and agriculture is being extended onto new soils that are high in organic matter, the decay of humus is accelerated. The extent of the acceleration is not known; it might be as high as the release through direct harvest of forests.

Recent Storage of Carbon in the Biota: The Regrowth of Forests

Countering these trends, it is possible that the relaxation of pressures on both agriculture and forests brought by widespread use of fossil fuels has allowed the regrowth of forests over substantial areas. Regrowth in the tropics appears limited at present, although extensive regrowth occurred in Venezuela in the late 19th and early 20th centuries according to Hamilton and his colleagues (*33, 34*). Adams *et al.* (*15*) suggested that reforestation in Paraná, Brazil, has taken place on about 10 percent of the area cleared. In São Paulo, reforestation increased recently to 20 percent of the cutting. There is evidence that a substantial fraction of the primary forest is being replaced by nonforest vegetation that has a very much lower biomass. In areas where reforestation has occurred the secondary forests, especially those harvested periodically, have a smaller biomass than the primary forests they replaced.

Data on regrowth of forests in the north temperate zone are also limited. One of the areas for which data are available is New England. A recent study of changes in the net primary production and biomass there (*39*) has suggested a general decline in biomass of trees from Colonial times through 1900, followed by a period of regrowth of forests. The regrowth was greatest, of course, in the more rural states; it was least in the more urbanized southern New England states. The original forest had a standing crop of

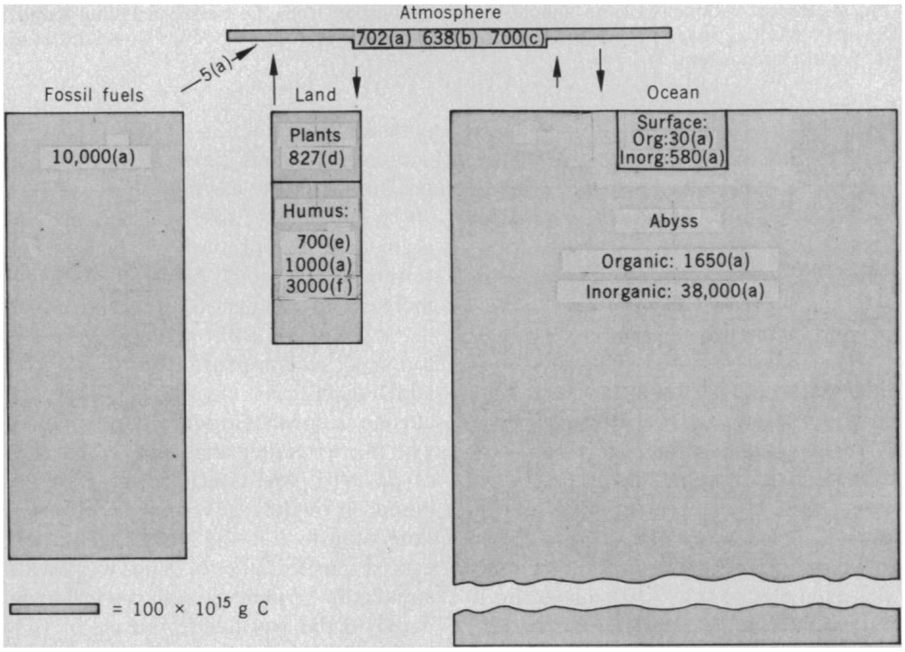

Fig. 2. The world carbon budget. The sizes of the boxes and arrows indicate the relative magnitudes of pools and flows. Oceanic sediments (not shown) probably contain more than $20{,}000{,}000 \times 10^{15}$ g. Sources of data are: (a) Baes *et al.* (*4*, p. 10); (b) SCEP (*1*, p. 16); (c) Bolin (*5*); (d) Whittaker and Likens [in (*3*), p. 283]; (e) Reiners and Wright (*16*); and (f) Bohn (*29*).

Table 1. Major plant communities of the earth and their area, net primary production, and standing crop [adapted from Whittaker and Likens (*23*)]. All values in column 4 are expressed as carbon on the assumption that the carbon content is ~0.45 of the dry matter.

Ecosystem type	Area (10^6 km^2)	Total net primary production of carbon (10^{15} g/year)	Total plant mass of carbon (10^{15} g)
Tropical rain forest	17.0	16.8	344
Tropical seasonal forest	7.5	5.4	117
Temperate evergreen forest	5.0	2.9	79
Temperate deciduous forest	7.0	3.8	95
Boreal forest	12.0	4.3	108
Woodland and shrubland	8.5	2.7	22
Savanna	15.0	6.1	27
Temperate grassland	9.0	2.4	6.3
Tundra and alpine meadow	8.0	0.5	2.3
Desert scrub	18.0	0.7	5.9
Rock, ice, and sand	24.0	0.03	0.2
Cultivated land	14.0	4.1	6.3
Swamp and marsh	2.0	2.7	13.5
Lake and stream	2.0	0.4	0.02
Total continental	149	52.8	827
Open ocean	332	18.7	0.45
Upwelling zones	0.4	0.1	0.004
Continental shelf	26.6	4.3	0.12
Algal bed and reef	0.6	0.7	0.54
Estuaries	1.4	1.0	0.63
Total marine	361	24.8	1.74
Full total	510	77.6	828

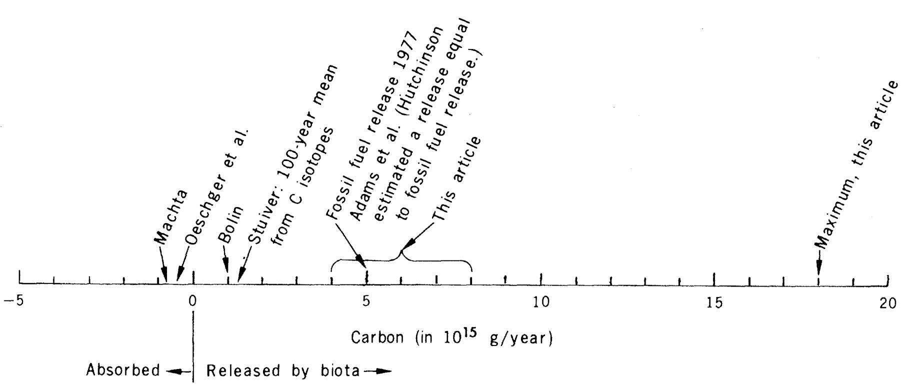

Fig. 3. Recent estimates of the annual release of carbon from the biota, including humus. Sources: Machta [in (*3*)]; Oeschger *et al.* (*27*); Bolin (*14*); Stuiver pre-1950 (*44*); Adams *et al.* (*15*); and Hutchinson (*13*).

about 2.5×10^{15} g of carbon. In 1900 the standing crop was estimated as 0.9×10^{15} g. The recovery during the ensuing 70 years increased the standing crop by about 0.3×10^{15} g, to about 1.2×10^{15} g. After 70 years of recovery the total standing crop was slightly less than 50 percent of the original biomass.

There have been no similar studies of other segments of the temperate and boreal zones. Maine is probably more nearly representative of rural forested areas in the transition from temperate to boreal forest than other segments of New England. The increment of storage of carbon in Maine during the period of recovery was estimated as 0.1×10^{15} g over the 70 years or 1.4×10^{12} g of carbon per year (*39*). If we assume that the increment of humus doubled this storage, the total carbon removed from the atmosphere was about 2.8×10^{12} g annually. If the experience in Maine is taken as representative of the forests of the temperate zones, storage in reforested lands has been less than 0.5×10^{15} g annually (*40*).

Carbon Dioxide Stimulation of Photosynthesis

There is an appreciable body of evidence that shows that increasing the concentration of CO_2 in air results in a stimulation of photosynthesis. The topic has been reviewed in detail by Lemon (*8*) with special attention to the possibility that there has been a worldwide stimulation of photosynthesis. Considering physiological response and using indirect arguments, Lemon concluded that the effect of increasing CO_2 on global photosynthesis is probably very small. If we assume that the net primary production of the biota is linearly proportional to the CO_2 concentration in air, then the increase in carbon storage to be expected annually would be the annual increase in the CO_2 content of air (0.8 ppm) expressed as a fraction of the total CO_2 content (330 ppm), times the net primary production of the earth $(0.8/330) \times 78 \times 10^{15}$ g of carbon (Table 1). The annual increment of net primary production due to this source would result in an annual increase in storage of not more than 0.2×10^{15} g of carbon; the increase is too small to compensate for the carbon added from forest clearing (*9*). This conclusion is consistent with Lemon's analysis (*8*), an earlier analysis by Broecker *et al.* (*10*), the conclusions of others based on models (*11*), and the observations of growth in the New England forests discussed above. The worldwide stimulation of plant growth is small compared to the worldwide release of CO_2 from industry and forest clearing.

Analysis Based on Metabolic Activity

The importance of atmospheric exchange of CO_2 with the terrestrial biota is further indicated by the seasonal oscillation in the CO_2 content of the atmosphere. Arctic and temperate zone and other seasonal vegetation store carbon over the period of the year that is unfavorable for growth. This storage is not characteristic of wet tropical forests that do not have a seasonal pulse.

The seasonal change in the CO_2 content of air is the product of the total respiration of various ecosystems, including man-dominated ones, and the gross production of the plant communities. Gross production in middle latitudes is heavily seasonal; there is very little in winter. Respiration continues throughout the year, but at different rates in winter and summer. The difference between the two processes is the net amount of carbon stored in or released from the ecosystem at any time. The storage follows in pattern the seasonal oscillation observed in the CO_2 content of the atmosphere. The peak concentration of CO_2 in air occurs in late winter or spring; the minimum, in late summer or fall. There seems to be little doubt that the oscillation is related to the annual cycle of metabolism of the vegetation.

Hall *et al.* (*41*) tested the hypothesis that if there had been changes over the last 15 years in the net primary production of the Northern Hemisphere relative to total respiration, the changes should appear as a change in the amplitude of the winter-to-summer oscillation observed in the Mauna Loa data (Fig. 1). An increase or reduction in amplitude would imply a change in the storage of carbon in the biota. The analysis by Hall *et al.* showed no such change that was significant. A similar analysis of a 10-year span of data from Brookhaven, New York, showed a trend toward reduced amplitude in later years, but again the trend was not significant (*42*). These results are probably not surprising in view of the short span of the data from Mauna Loa and Brookhaven. Nonetheless, if there had been a drastic change (more than 10 percent) in net primary production relative to total respiration in the middle latitudes of the Northern Hemisphere during this period, one would expect to be able to recognize it through such analyses.

Appraisals Based on Carbon Isotope Ratios

One of the most attractive techniques for appraising indirectly the contribution of the biota and fossil fuels to the current pool of carbon in the atmosphere is comparison of the ratios of the carbon isotopes ^{12}C, ^{13}C, and ^{14}C. The technique exploits the fact that the ratios differ among the major interacting pools of carbon: fossil fuels contain no ^{14}C and are enriched in ^{12}C relative to ^{13}C. The contemporary biota contains ^{14}C and is also enriched in ^{12}C compared to the atmosphere. Combustion of fossil fuels releases carbon that is impoverished in ^{14}C and dilutes the ^{14}C of the atmosphere. This dilution is called the Suess effect (*43*). The Suess effect for ^{14}C is not in itself sufficient to distinguish between biotic release of carbon and fossil release because the biotic pool is in relatively short-term equilibrium with the atmosphere and has substantially the same ^{14}C content. The Suess effect for ^{14}C, however, can be used with the $^{12}C/^{13}C$ ratios to estimate the biotic release.

Using samples of cellulose from the stem of a tree whose annual increments of wood could be dated with precision, Stuiver (*44*) has shown that the carbon isotope ratios in the cellulose suggest that between 1850 and 1950 there was an average annual release of about 1.2×10^{15} g of carbon from the biota. The average fossil fuel release in that period was 0.6×10^{15} g. Stuiver's 100-year average rate for release of carbon from the biota would be expected to be above the actual rate at the beginning of this period and below it toward the end, after the growth of industrialization and population that marked that century.

Table 2. Estimates of current releases of carbon from major terrestrial plant communities. Releases from forests were calculated as shown in (*45*). Column 5 gives what we consider to be the most probable limits based on a maximum of twice the net release and a lower limit of one-third the net release.

Plant community	Carbon released ($\times 10^{15}$ g)			
	Forest clearing and harvest	Increased NEP	Net release	Range
Tropical forests	4.4	0.9	3.5	1–7
Temperate zone forests	1.7	0.3	1.4	0.5–3
Boreal forest	1.0	0.2	0.8	0–2
Other vegetation (including agriculture)	0.3*	0.1	0.2	0–1
Total land vegetation	7.4	1.5	5.8	1.5–13
Detritus and humus			2.0†	0.5–5.0
Land total			7.8	2–18

*The major contributions to a release are from woodlands and savannas that are cleared for agriculture or grazing. We have assumed a clearing rate of 0.6 percent of these lands, with about one-third of that restored as increased NEP. †Major releases from organic detritus and humus are probably in the clearing of forest for agriculture or for grazing, although there are substantial releases associated with harvests of timber (*38*).

Sources and Sinks for Carbon Dioxide

These various approaches to estimating the role of the biota in the world carbon budget are consistent in that none suggests that the biota is or has been an appreciable sink for carbon. The evidence is overwhelming that the trend throughout the past two millennia has been for a more or less steady reduction in the earth's forests. The evidence for contemporary changes is more equivocal. We can use the interpretations offered above with the data of Table 1 and data on rates of harvest from the literature to estimate current releases. Table 2, which was derived in this way, is little more than a guide to indicate the relative magnitudes of contributions from various segments of the world vegetation.

In preparing Table 2 the annual rate of clearing of forests and transfer to agriculture, grazing, or to other vegetation of lesser stature was assumed to be 1 percent of the 1950 biomass. We estimated that 5 percent of the biomass might be stored in structures. Increased rates of storage [net ecosystem production (NEP) (*45*)] would also occur as primary forests with very low NEP were turned into successional forests with a higher NEP. With the data available it was not possible to be more precise. We judge that the range of 0.5 to 1.0 percent per year includes the correct current rate of clearing of tropical forests and that the most probable range for the total world release from the biota annually is 4 to 8×10^{15} g of carbon.

Several recent estimates of the world carbon budget are summarized in Fig. 3. Apart from values from models (*25–27*), current estimates for the annual release of carbon range from $1.0 \pm 0.6 \times 10^{15}$ g (*5*) to our maximum range of 2 to 18×10^{15} g. A middle range of 4 to 8×10^{15} g includes the values suggested by Adams *et al.* (*15*) and Hutchinson (*13*).

Sinks. If the current appraisals are correct, the contemporary biotic release of carbon is approximately equal to the fossil fuel release. The total for both sources may exceed 10^{16} g annually. Of this about 2.3×10^{15} g accumulates in the atmosphere. The remainder probably enters the oceans, but the mechanism for this remains puzzling. The apparently erroneous assumption that the biota is a contemporary sink for CO_2 arose because the data on oceanic mixing seem to show that the oceans have a limited capacity for absorbing CO_2 in the short run of years or decades (*10, 44*) and other sinks have seemed necessary. The problem is still more puzzling if the biota not only is not a sink for fossil fuel carbon but is an additional source of CO_2. The validity and appropriateness of the models of oceanic mixing are obviously in question; so are the assumptions that biotic processes do not result in substantially greater transfers of carbon into the deeper waters of the oceans. Human activities along the continental margins result in the accelerated sedimentation of carbon fixed on land on the continental shelves, but the amount sequestered in this way is probably too small to be a major sink for carbon.

Questions remain as to the possibility of additional terrestrial sinks as well as the size of the terrestrial source of CO_2. Various hypotheses have been advanced, including the possibility that the retreat of glacial ice is allowing a northward advance of the tundra and boreal forest with significant storage of carbon. Few such hypotheses can be ruled out unequivocally, but there appears to be no single major sink for carbon equivalent to the releases estimated here except the oceans (Table 1). Certainly, there is need for additional and better information on the year-by-year changes in the carbon held in the major vegetation types of the earth with special emphasis on forests. Such data can be compiled by a variety of techniques, including aerial and satellite photography. There is also a need for intense examination of the flux of carbon into the oceans. One possibility is that biotic mechanisms in the oceans are more effective than has been assumed in transferring fixed carbon into the deeper oceanic waters.

The greatest puzzle is the basic stability of the global carbon budget. Why have human activities, which are recognized as having large effects on major segments of this basic series of chemical cycles, not brought greater changes in the CO_2 content of air? The answers are obviously complicated; they will come through intensified research on the global carbon cycle.

References and Notes

1. Report of the Study of Critical Environmental Problems (SCEP), *Man's Impact on the Global Environment* (MIT Press, Cambridge, Mass., 1970).
2. Report of the Study of Man's Impact on Climate (SMIC), *Inadvertent Climate Modification* (MIT Press, Cambridge, Mass., 1971).
3. G. M. Woodwell and E. V. Pecan, Eds., *Carbon and the Biosphere* (AEC Technical Information Center, Washington, D.C., 1973).
4. C. F. Baes, H. E. Goeller, J. S. Olson, R. M. Rotty, *Am. Sci.* **65**, 310 (1977).
5. B. Bolin, *Sci. Am.* **223**, 124 (September 1970).
6. There have been several recent conferences whose proceedings have not yet been published. These include the 1976 symposium in the *Symposium Series in Oceanography* of the U.S. Office of Naval Research; the ERDA Conference on the World CO_2 Problem in Miami, Florida, March 1977; and the ICSU-SCOPE Conference on the World Carbon Budget in Ratzeburg, West Germany, in April 1977. The December 1976 Dahlem Conference has been published recently (*7*).
7. W. Stumm, Ed., *Dahlem Conference in Biogeochemistry* (Dahlem Konferenzen, Berlin, 1977).
8. E. Lemon [in *Symposium Series in Oceanography* (Office of Naval Research, Washington, D.C., in press)] concluded that while increased CO_2 in air may stimulate photosynthesis when other factors are not limiting, there has probably been very little change in world rates of photosynthesis as a result of the estimated 10 percent increase in CO_2 in the atmosphere since the middle of the last century. See also (*10, 11*).
9. This amount represents only the maximum annual increase in net primary productivity due to the increase in CO_2 in air. A larger increase in NPP might result from the accumulated increase in CO_2, about 10 percent during the last 30 years.

Much of the increase in NPP would, however, be in short-lived tissues that do not accumulate from year to year; that part of increased NPP going into woody tissues would be subject to death and decay, and the full amount of that increased woody NPP would not accumulate in storage as biomass. We know of no evidence of increased wood storage in natural forests because of CO_2 increases, but have no way to calculate with assurance the possible effect.

10. W. S. Broecker, Y. H. Li, T. H. Peng, in *Impingement of Man on the Oceans*, D. W. Hood, Ed. (Wiley, New York, 1971), p. 292.
11. D. B. Botkin, J. F. Janak, J. R. Wallis, in (*3*); D. B. Botkin, *BioScience* **27**, 235 (1977).
12. G. M. Woodwell and R. A. Houghton, in (*7*).
13. G. E. Hutchinson, in *The Earth as a Planet*, G. P. Kuiper, Ed. (Univ. of Chicago Press, Chicago, 1954), p. 390.
14. B. Bolin, *Science* **196**, 613 (1977).
15. J. A. S. Adams, M. S. Mantovani, L. L. Lundell, *ibid.*, p. 54.
16. W. A. Reiners and H. E. Wright, Jr., in (*7*).
17. C. W. Brown and C. D. Keeling, *J. Geophys. Res.* **70**, 6077 (1965); J. C. Pales and C. D. Keeling, *ibid.*, p. 6053; C. D. Keeling, J. A. Adams, Jr., C. A. Eckdahl, Jr., P. R. Guenther, *Tellus* **28**, 552 (1977); C. D. Keeling, R. B. Bacastow, E. A. Bainbridge, C. A. Eckdahl, Jr., P. R. Guenther, L. S. Waterman, J. F. S. Chin, *ibid.*, p. 538.
18. C. A. Eckdahl and C. D. Keeling, in (*3*), pp. 51–85.
19. G. M. Woodwell, R. A. Houghton, N. R. Tempel, *J. Geophys. Res.* **78**, 932 (1973).
20. C. D. Keeling, *Tellus* **25**, 174 (1973).
21. W. Bischoff and B. Bolin, *ibid.* **18**, 155 (1966); B. Bolin and W. Bischoff, *ibid.* **22**, 431 (1970).
22. B. Bolin and C. D. Keeling, *J. Geophys. Res.* **68**, 3899 (1963).
23. R. H. Whittaker and G. E. Likens, in (*3*), pp. 281–302.
24. ______, in *Primary Productivity of the Biosphere*, H. Lieth and R. H. Whittaker, Eds. (Springer-Verlag, New York, 1975), pp. 281–302.
25. Study of Critical Environmental Problems (*1*); Machta *et al.* (*26*); C. D. Keeling, in *Chemistry of the Lower Atmosphere*, S. I. Rasooi, Ed. (Plenum, New York, 1973), pp. 21–31; R. Bacastow and C. D. Keeling, in (*3*); L. Machta, in (*3*); Oeschger *et al.* (*27*). Broecker *et al.* (*10*) did not make this assumption in their excellent discussion of the carbon problem.
26. L. Machta, K. Hanson, C. D. Keeling, unpublished manuscript.
27. H. Oeschger, U. Siegenthaler, U. Schotterer, A. Gugelmann, *Tellus* **27**, 168 (1975).
28. The most recent appraisal is that of Baes *et al.* (*4*).
29. H. L. Bohn, *Soil Sci. Soc. Am. J.* **40**, 468 (1976).
30. H. C. Darby, in *Man's Role in Changing the Face of the Earth*, W. L. Thomas, Ed. (Univ. of Chicago Press, Chicago, 1956), vol. 1, p. 203.
31. E. P. Eckholm, *Losing Ground* (Norton, New York, 1976).
32. Although Bolin used 0.8×10^{15} g of carbon per year as the net release from forests (*14*, table 3, p. 614), his data suggest a release from African and South American forests of 1.6×10^{15} g by one calculation and 2.4×10^{15} g by another (*14*, p. 614).
33. J. P. Veillon, in (*34*), pp. IV-1 to IV-17.
34. L. S. Hamilton, *Tropical Rainforest Use and Preservation: A Study of Problems and Practices in Venezuela* (Sierra Club, Washington, D.C., 1976).
35. Data from the FAO provided through the World Wildlife Fund, Morges, Switzerland, showed a world reduction in the area of rain forest from an original 15.92×10^6 to a current 9.35×10^6 km². The current rate of harvest is estimated as 0.11×10^6 km² or 1.12 percent annually.
36. R. J. A. Goodland and H. S. Irwin, *Amazon Jungle: Green Hell to Red Desert?* (Elsevier, New York, 1975). See also T. B. Croat, *BioScience* **22**, 465 (1972); A. Gómez-Pompa, C. Vásquez-Yames, S. Guevara, *Science* **177**, 762 (1972); H. Sioli, in *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*, B. S. Meggers, E. Ayensu, D. Duckworth, Eds. (Smithsonian Institution, Washington, D. C., 1973), pp. 321–334.
37. W. A. Reiners, in (*3*), pp. 303–327; W. H. Schlesinger, *Annu. Rev. Ecol. Syst.* **8**, 51 (1977).
38. There is a considerable background of experience with changes in the humic content of soils under cultivation. Under most circumstances cultivation results in losses of organic matter [for instance, see C. Lee and R. H. Bray, *Soil Sci.* **68**, 203 (1949)]. In tropical forest soils similar losses occur when the shift is made to agriculture [P. H. Nye and D. J. Greenland, *The Soil Under Shifting Cultivation* (Commonwealth Bureau of Soils, Harpenden, England, 1960)]. Recent studies of New England forest soils following harvest of timber also show substantial losses of organic matter that extend through the early years of succession following the harvest [W. W. Covington, dissertation, Yale University (1977)]. The worldwide estimates are little more than guesses, however.
39. T. Wood and D. B. Botkin, *Am. Sci.*, in press.
40. The annual net storage in Maine over the 70 years appears to have been not more than 2 to 3 percent of the net primary production. These forests have been harvested continuously over that period, of course. The potential storage of carbon from year to year probably does not exceed about 50 percent of the net primary production.
41. C. A. S. Hall, C. A. Eckdahl, D. E. Wartenberg, *Nature (London)* **225**, 136 (1975).
42. G. M. Woodwell and R. A. Houghton, unpublished data.
43. H. E. Suess, *Science* **122**, 415 (1955).
44. M. Stuiver, *ibid.*, in press.
45. Net ecosystem production is the net storage (or loss) of carbon by a unit of landscape. It drops to zero when total respiration equals gross production in old-growth forests and is normally positive during midsuccession in forest seres [G. M. Woodwell and R. H. Whittaker, *Am. Zool.* **8**, 19 (1968)]. Sample calculation: The plant biomass of tropical forests was estimated as 461×10^{15} g of carbon (Table 1). If 1 percent of old-growth forest were cut per year, 4.6×10^{15} g of carbon per year could be released as CO_2. However, some 5 percent of this, or 0.2×10^{15} g, might go into long-term storage in structures and thus only 4.4×10^{15} g per year would be released. If 10 percent of tropical forests have been cut, and half of this area now supports forest regrowth, the carbon going into storage in that regrowth would equal tropical forest productivity, estimated to total 22×10^{15} g of carbon per year (Table 1), times ½ of 10 percent, times 0.6 of that productivity that goes into woody tissues, or 0.66. If the regrowing forests have a net production 1.4 times greater than the old-growth forests, the amount into storage (increased NEP) would be about 0.9×10^{15} g of carbon, and the net release of carbon as CO_2 would be $4.6 - 0.2 - 0.9 = 3.5 \times 10^{15}$ g of carbon per year.
46. In preparing this article we have had the advantage of extensive discussions with various colleagues at the series of meetings held over recent months, including the Dahlem Conference in West Berlin, the Conference on the World Carbon Budget in Ratzeburg, West Germany, and the Miami Beach Conference arranged under ERDA auspices. Individuals who have contributed to these discussions include B. Bolin, E. Ericsson, E. Degens, R. Rotty, E. Lemon, L. Machta, W. Broecker, A. Weinburg, H. Brooks, and others. Research supported by the Ecosystems Center, Marine Biological Laboratory, Woods Hole, Mass.

Phosphorylated Proteins as Physiological Effectors

Protein phosphorylation may be a final common pathway for many biological regulatory agents.

Paul Greengard

Within the past few decades, the individual steps in many essential metabolic pathways have been elucidated. In contrast, we are only now beginning to understand the homeostatic mechanisms by which multicellular organisms regulate and coordinate their metabolic and physiological processes in the face of a constantly changing internal and external environment. An understanding of such systems would clearly be of great importance for our comprehension of basic biological processes. In addition, such information would be of profound medical significance. It seems probable that derangements of homeostatic processes are responsible for many disease states. Conversely, it seems likely that the effects of many therapeutic and toxic agents are exerted on such homeostatic systems. In this article I outline a conceptual framework within which many features of biological regulation may be understood. This framework attributes a role of central importance to phosphorylated proteins in the control of diverse biological processes.

About 10 years ago, a cyclic AMP (adenosine 3′,5′-monophosphate)-dependent protein kinase was discovered in skeletal muscle, and evidence was presented that this protein kinase mediates the effects of cyclic AMP in causing the breakdown of glycogen (*1*). Sub-

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