

The flux of carbon from terrestrial ecosystems to the atmosphere in 1980 due to changes in land use: geographic distribution of the global flux

By R. A. HOUGHTON, R. D. BOONE¹, J. R. FRUCI, J. E. HOBBIE, J. M. MELILLO, C. A. PALM², B. J. PETERSON, G. R. SHAVER and G. M. WOODWELL³, *The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, USA*; B. MOORE and D. L. SKOLE, *Complex Systems Research Center, University of New Hampshire, Durham, NH 03824, USA*; and N. MYERS, *Upper Meadow, Old Road, Headington, Oxford OX3 8SZ, England*

(Manuscript received December 10, 1985; in final form July 21, 1986)

ABSTRACT

Recent analyses of land-use change in the tropical regions and in the temperate and boreal regions of the earth were combined to yield a global estimate of $1.0 - 2.6 \times 10^{15}$ g C for the net release of carbon to the atmosphere in 1980 from changes in land use. Deforestation in the tropics accounted for nearly all of the flux; the net release of carbon from temperate and boreal regions was only 0.1×10^{15} g C. The average global value of 1.8×10^{15} g C in 1980 was distributed geographically among tropical countries and other regions on the basis of deforestation rates and carbon stocks.

The net release of carbon from changes in land use worldwide is inconsistent with the results of geochemical models of the carbon cycle. The discrepancy is smaller than in previous analyses, but is large enough to exceed the errors of the analysis. Possible explanations for the discrepancy include the possibility of a net accumulation of carbon in undisturbed ecosystems as a result of CO₂ fertilization or changes in climate. Even if the terms of the global carbon equation were to appear balanced at present, current knowledge is insufficient to predict whether terrestrial ecosystems will act as a positive or negative feedback on the anticipated CO₂-caused global warming.

1. Introduction

Recent estimates of the release of carbon from terrestrial ecosystems as a result of deforestation and reforestation range between 1.0 and 2.6×10^{15} g C for the years around 1980 (Houghton et al., 1985b). These estimates are higher than can be accommodated by most models of the carbon cycle that satisfy geophysical and geochemical constraints. The discrepancy

might be resolved, or at least more precisely defined, through an examination of the geographic variability in the sources and sinks of carbon with three-dimensional atmospheric transport models that are consistent with the observed concentrations of CO₂ in air (Pearman and Hyson, 1980; Fung et al., 1983; Heimann and Keeling, 1985, pers. comm.). If estimates of the global fluxes of CO₂ between the atmosphere and fossil fuels, the oceans, and the terrestrial biota could be distributed among geographic regions, the location of the global imbalance might be identified and the reasons for the discrepancy made clearer.

The purpose of this paper is to determine the geographic distribution of the biotic flux of carbon in 1980 produced as a result of changes in

¹ Present address: Department of Forestry, University of Massachusetts, Amherst, MA 01003, USA.

² Present address: Department of Soil Science, North Carolina State University, Raleigh, NC 27650, USA.

³ Present address: Woods Hole Research Center, Woods Hole, MA 02543, USA.

land use, for example, deforestation, reforestation, logging and changes in agricultural area. Two earlier papers calculated the net flux from broad regions within the tropics (Houghton et al., 1985a) and within the temperate and boreal zones (Melillo et al., 1985, pers. comm.). This paper combines the results of these previous analyses to create a global estimate and disaggregates the regional estimates into country-specific estimates of the net flux. Countries were used as the geographic unit in the tropics because rates of deforestation in the tropics are given by country. Where possible the estimated net flux of carbon has been distributed with greater geographic resolution; in the temperate and boreal zones the resolution is more coarse. The results can be reaggregated to fit various scales of geographic resolution required by different models.

2. Methods

2.1. General

The greatest changes in terrestrial carbon result from the transformation of forests to non-forests and from the transformation of non-forests to forests. The net change in terrestrial carbon or the net flux of carbon between land and the atmosphere depends on the rates at which carbon is lost to the atmosphere from burning and decay of dead plant material and from oxidation of soil organic matter, and the rates at which carbon is removed from the atmosphere through growth of live vegetation and accumulation of soil organic matter. Rates of decay and regrowth vary with the type of ecosystem and the type of land use. Fifteen types of ecosystems, including nine tropical and six temperate and boreal ecosystems (Appendices 2, 7), and six types of land use (Appendices 3, 5–7) were included in the analyses reported here. The model used to calculate the net flux of carbon between terrestrial ecosystems and the atmosphere was the same as described by Moore et al. (1981) and Houghton et al. (1983) with the exception that for this paper the analyses included shifting cultivation in the tropics (see below and Palm et al. (1986)). The data used to obtain the estimates of flux are given in Appendices 1–11. Terrestrial ecosystems not directly modified by man's activities were assumed to be in steady

state with respect to carbon. The potential errors from this assumption are discussed below.

2.2. Temperate and boreal ecosystems

The data used to calculate the net flux of carbon between the ecosystems of the temperate and boreal zones and the atmosphere were modified in two ways from those reported by Houghton et al. (1983). First, the analysis for the Soviet Union was revised to include more detailed information on land use (Melillo et al., 1985, pers. comm.) (Appendices 1–6). The work divided the USSR into a region east of the Ural Mountains where little agricultural or logging activity took place until recently and a region west of the Urals where logging practices have been intensive. The study distinguished between harvest of forests for industrial wood (largely lumber products) and harvest for non-industrial wood (largely fuelwood). The former (lumber) is generally more intensive and may involve clear cutting; the latter (fuel) leaves much of the original forest intact.

The second revision of the analysis by Houghton et al. (1983) was a reduction in the loss of carbon from soils after disturbance. The loss of carbon from the top 1 m of soil following wood harvest and clearing for cultivation was modelled as 20% and 25%, respectively (Appendices 1, 2). In the earlier analysis reductions of 50% were assumed for both harvest and clearing for crops, but a recent review of the literature suggests that lower values are more typical (Schlesinger, 1986).

As a result of these modifications, the net flux of carbon from those regions generally outside the tropics was estimated to be about 0.1×10^{15} g in 1980 (Table 1), lower than the net flux calculated earlier (0.5×10^{15} g C) (Houghton et al., 1983). The new value is believed to be a more accurate estimate of the net flux than the flux calculated for the vegetation of harvested forests alone by Armentano and Ralston (1980) and Johnson and Sharpe (1983) because the new estimate considers, in addition to regrowing vegetation, the changes in soil carbon associated with harvest and regrowth, the oxidation of harvested wood, and the loss of carbon from increases in cultivated area (Table 2).

The only geographic partitioning made among these temperate and boreal regions was to divide the USSR into western and eastern sectors and to

Table 1. Net flux of carbon (10^{12} g) in 1980 from land-use changes in the temperate and boreal regions of the earth; negative values indicate a net storage of carbon on land; subtropical regions of China and Australia are included

	Increase* in croplands	Abandonment of croplands	Harvest† and regrowth	Afforestation	Oxidation of wood products	Total
USA and Canada	4	-7	-68	0	96	25
Europe	2	-29	-49	-3	51	-28
USSR						
West	31	-23	-33, -6	-4	35	0
East	30	0	-1, -2	-3	11	35
Japan and Korea	0	0	-10	0	7	-3
China	41	0	42	-28	14	69
North Africa and Middle East	2	0	4	0	1	7
Total for temperate and boreal systems of northern hemisphere	110	-59	-123	-38	215	105
Australia and New Zealand	24	0	-6	0	10	28
Total for all temperate and boreal ecosystems	134	-59	-129	-38	225	133

* A net release of carbon in 1980 does not necessarily mean an increase in croplands in 1980; the net release may result from oxidation of soils first cultivated before 1980.

† For harvests in the USSR, the first value refers to a net flux of carbon from harvest of industrial wood, the second value refers to the net flux of carbon from harvest of non-industrial wood (largely fuelwood).

Table 2. Comparison of estimates of the net flux of carbon (10^{15} g) between the temperate and boreal regions of the earth and the atmosphere due to changes in land use; subtropical regions of China and Australia are included in the estimates by Melillo et al.; negative values indicate a net storage of carbon on land

	Harvest and regrowth of forests					Total
	Regrowth of forest vegetation	Oxidation and recovery of soil organic matter	Oxidation of slash left on site	Oxidation of wood products	Expansion and abandonment of croplands	
Melillo et al. (1985, pers. comm.)	-1.00	0.10	0.64	0.30	0.09	0.13
Armentano and Ralston (1980)	-1.0 to -1.2					-1.0 to -1.2
Johnson and Sharpe (1983)	-1.6 to -1.9					-1.6 to -1.9

divide the Pacific Developed region into a northern hemispheric component, Japan and the two Koreas, and a southern hemispheric component, Australia and New Zealand (Table 1).

2.3. Tropical forests

Much of the clearing of forests for agriculture in the tropics is cyclic because the practice of

shifting cultivation allows forests to regrow on fallow lands during and following the harvest of food crops (Fig. 1). The cycle begins with the burning of a plot of forest. Some of the larger trees are often left standing. Felled wood is used for local building and for cooking. Food crops are planted in the ashes and harvested for periods of one to ten years. The yields generally decline over

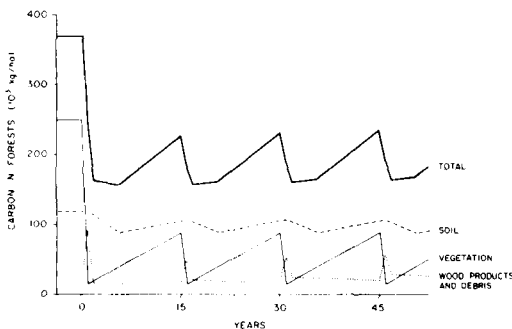


Fig. 1. Changes in the carbon in live vegetation, soil organic matter, and woody debris during three cycles of shifting cultivation (from Houghton et al. (1985a)).

time as the forest grows back and soil fertility is reduced. Some of the surface organic matter is oxidized during the burn and in the earliest years of cropping. The soil organic matter develops again as the forest regrows. The period of fallow, after which the forest may be burned and cleared again, may last from 3 to 80 years depending on cultural and environmental conditions.

Shifting cultivation was not explicitly included in the earlier analysis by Houghton et al. (1983), although some of the high rates of forest clearing used in the analyses mistakenly included areas of shifting cultivation in the estimates of permanent clearing of forests for agriculture. A model of shifting cultivation has since been developed and was included in the analyses presented here. The model is similar to the model for forest harvest in that cohorts of land area are followed through time and calculated to accumulate or lose carbon according to rates of oxidation and growth (Fig. 1 and Appendices 7, 8).

Over the long term, a constant rate of deforestation for shifting cultivation will not contribute a net flux of carbon to the atmosphere. Carbon released to the atmosphere during burning balances the carbon accumulating in regrowth. In recent years, however, the area of forests cleared annually for shifting cultivation has increased (FAO/UNEP, 1981a, b, c), the rotation length has been reduced, and the area of fallow forests may also have decreased as fallow lands are cleared for permanent use (Myers, 1980, 1984; Houghton et al., 1985a). All of these trends have increased the net release of carbon from the tropics.

Estimates of the net flux of carbon from deforestation in the tropics vary between 0.5 and 1.7×10^{15} g C yr⁻¹ (Molofsky et al., 1984; Detwiler et al., 1985; Houghton et al., 1985a). For these estimates, deforestation is limited to the loss of undisturbed, logged, managed, or unproductive forests, as defined and estimated by FAO/UNEP (1981a, b, c). When Myers' data (1980, 1984) on the permanent clearing of fallow lands are included in the analyses, estimates of the biotic flux of carbon are increased by 0.4 to 0.8×10^{15} g C yr⁻¹ to a more likely range of 0.9 to 2.5×10^{15} g C yr⁻¹ for the tropics (Houghton et al., 1985a). Uncertainties in the rates of deforestation, in the carbon stocks of the forests cleared, and in the permanence of the deforestation contribute about equally to this range. The rates of tropical deforestation, permanent and temporary, used to obtain the range of flux estimates 0.5 to 1.7×10^{15} g C yr⁻¹ are given in Appendices 9–11. The rates of deforestation were derived from FAO/UNEP (1981a, b, c), Myers (1980, 1984) and the Production Yearbooks (FAO, 1983). The lower estimates of carbon stocks used in the analyses were those calculated by Brown and Lugo (1984) on the basis of wood volumes given in the FAO/UNEP study (1981a, b, c); the higher estimates were based on direct measurements of biomass compiled by Brown and Lugo (1982) (Appendix 7).

The regional fluxes calculated by Houghton et al. (1985a) were disaggregated for this study on the basis of country-specific data given in FAO/UNEP (1981a, b, c). An index of carbon release was determined for each country as the product of deforestation rate (FAO/UNEP, 1981a, b, c, their Table 6) $\times$ growing stocks (FAO/UNEP, 1981a, b, c, their Table 4). The three categories of forests considered by FAO/UNEP, undisturbed, logged, and unproductive, were used to compute the index. Countries with higher rates of deforestation or larger volumes of growing stocks yielded a greater index and, hence, accounted for a larger fraction of the regional flux of carbon than countries with lower rates of deforestation and lower growing stocks. The values of the regional fluxes were the mid-points of the ranges obtained with FAO/UNEP data: 0.497×10^{15} g C for tropical America, 0.283×10^{15} g C for tropical Africa, and 0.280×10^{15} g C for tropical Asia (Table 3).

Table 3. *Calculated net release of carbon to the atmosphere in 1980 (10^{15} g) from deforestation of non-fallow forests in the tropics (Houghton et al., 1985a)*

	FAO/UNEP	Myers	FAO
America	0.344 (0.649)	0.220 (0.400)	0.419 (0.783)
Africa	0.175 (0.390)	0.184 (0.406)	0.177 (0.394)
Asia	0.198 (0.362)	0.223 (0.486)	0.112 (0.190)
All tropics	0.717 (1.401)	0.627 (1.292)	0.708 (1.367)

The values in parentheses were obtained using estimates of carbon stocks based on direct measurements (Brown and Lugo, 1982). The other values were obtained using estimates of carbon stocks derived from volumes of wood reported by FAO/UNEP (1981a, b, c) (Brown and Lugo, 1984).

Finer resolution of deforestation within Brazil was possible from the results of studies by Tardin et al. (1980) and the Brazilian Institute of Forestry Development (IBDF, 1983) (from Fearnside (1984)). These studies reported rates of deforestation for nine states in Brazil's legal Amazonia. Legal Amazonia includes all of the states listed in Table 4 except parts of Goiás and Maranhão. The area includes about half of Brazil and all of the closed forests of the Amazon Basin. It does not include the closed forests of the Atlantic coast, and thus any deforestation there or in the open forests outside legal Amazonia is not included in this estimate of carbon flux. The sum of deforestation for the states of legal Amazonia was similar to FAO/UNEP's estimate of deforestation in open and closed forests, but the Brazilian studies did not distinguish between open and closed forests. The distinction is important here because the stocks of carbon in closed forests are typically three to five times higher than in open, or dry, forests (Appendix 7). Assignment of deforestation within states to open and closed forests was made proportional to the ratio of open (cerrado) to closed forest in each state (Anuario Estatístico do Brasil, 1979). Only four of the states contained significant areas of open forest and most of its deforestation was assumed to be in Mato Grosso. Errors introduced from these assumptions affect only the geographic distribution of the flux within Brazil and not the total net flux of carbon from that country.

Myers' (1980) survey of deforestation in the

tropics and a recent comparison of Myers' estimates with those of FAO/UNEP (Houghton et al., 1985a) suggest that the permanent clearing of fallow forests is responsible for an additional release of carbon (0.4 to 0.8×10^{15} g C yr⁻¹) not calculated from consideration of data in the FAO/UNEP study alone. This additional flux of carbon was not partitioned among tropical regions in the original study (Houghton et al., 1985a), but the average flux of 0.6×10^{15} g C was partitioned here among regions in proportion to Myers' estimates of the rates of deforestation by forest farmers (Myers, 1984). Within each region the flux was assigned to countries identified by Myers (1984) and was distributed among these countries in proportion to estimates of deforestation of closed forests (FAO/UNEP, 1981a, b, c) (Table 4).

3. Results and conclusions

The net biotic flux of carbon in 1980 due to changes in the use of land was estimated to be distributed geographically as shown in Tables 1, 4 and Fig. 2. The net global flux, $1.8 \pm 0.9 \times 10^{15}$ g C, was almost entirely from tropical regions in 1980. Only 0.1×10^{15} g C was calculated to have been released to the atmosphere from outside the tropics. With the exception of Europe, and perhaps Japan, Korea, and western USSR, the direction of the flux of carbon was from terrestrial ecosystems to the atmosphere.

The net release of carbon from terrestrial ecosystems to the atmosphere in 1980 is inconsistent with most geochemical models of the carbon cycle (e.g., Bacastow and Keeling, 1973; Oeschger et al., 1975) and raises the possibility that the release of carbon from deforestation, agricultural expansion, and other direct effects of man is counteracted by a net storage elsewhere. The excess or missing carbon (Broecker et al., 1979) is smaller than earlier studies suggested (Woodwell et al., 1978; Houghton et al., 1983), but a discrepancy on the order of 1 to 2×10^{15} g C yr⁻¹ still appears to exist (Keeling, Heimann, Mook, 1985, pers. comm.). The discrepancy could be resolved if either the oceans or the terrestrial biota were found to accumulate more carbon than presently thought.

There have been several mechanisms proposed

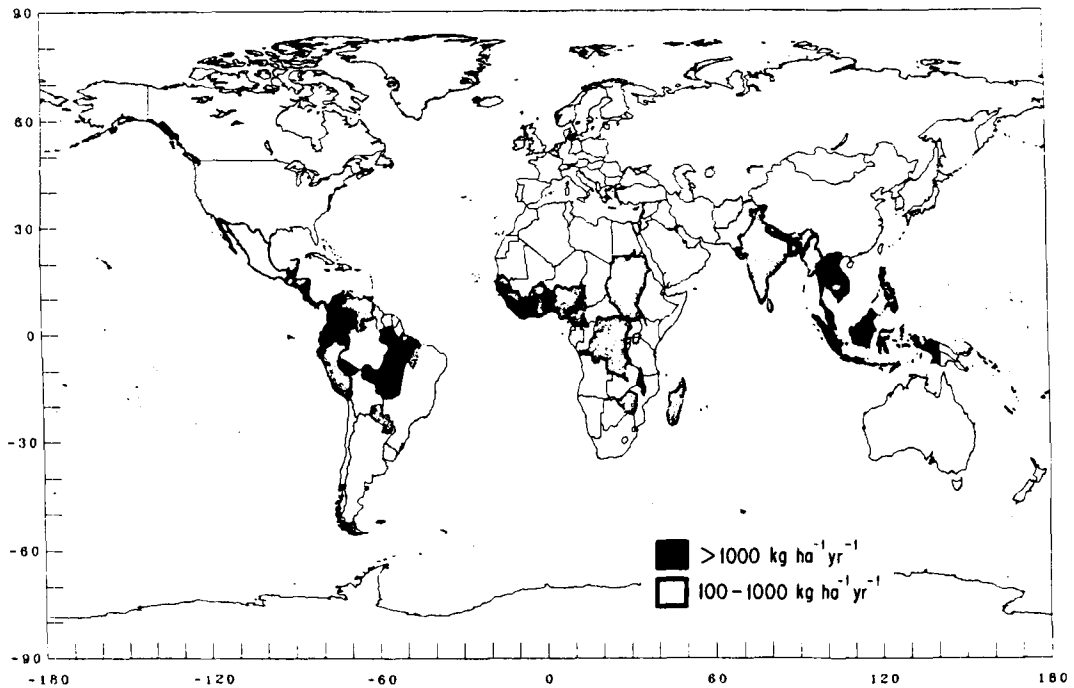


Fig. 2. Geographic distribution of the net flux of carbon from terrestrial ecosystems to the atmosphere in 1980 as a result of deforestation and agricultural expansion.

for storage of carbon by the biota. The first of these mechanisms, the storage of carbon in forests regrowing after harvest, agricultural abandonment, or afforestation, does not resolve the discrepancy because this analysis has included the regrowth of forests (cf., Molofsky et al., 1984; Detwiler et al., 1985; Houghton et al., 1985a; Melillo et al., 1985, pers. comm.). There are human impacts that cause a release of carbon to the atmosphere in addition to the releases reported in these analyses. The declining forests in central Europe (Bach, 1985) and the degradation of open forests throughout the tropics (FAO/UNEP, 1981) are examples of losses of carbon not included in the estimates of flux reported here. Thus, the range of 1.0 to 2.6×10^{15} g C for the world may be low.

On the other hand, the assumption that undisturbed systems are in steady state with respect to carbon storage is probably invalid. Arctic and boreal ecosystems, for example, are thought to be accumulating about 0.2×10^{15} g C annually (Miller, 1981; Miller et al., 1983).

Wetland soils in the temperate zone may also have stored carbon at approximately the same rate, but drainage of these lands for agriculture appears to have reversed the net flux of carbon (Armentano et al., 1984). Other systems may also be accumulating carbon but the rates in undisturbed systems must be either low ($<0.1 \times 10^{15}$ g C yr⁻¹) or short term (<200 years). Otherwise the stocks of carbon on land would be larger than observed.

That terrestrial systems not directly affected by man have been accumulating carbon during the past century is a possibility. The mechanism receiving greatest attention currently is the possibility that the increased concentration of CO₂ in air enhances photosynthesis and leads to an increased storage of carbon in plants or soil (Gifford, 1980; Lemon, 1983; Oechel and Strain, 1985). While there is abundant evidence that photosynthesis and growth are enhanced by elevated levels of CO₂ when essential nutrients are not limiting, some experimental evidence suggests that the limiting nutrients prevent plants

Table 4. *Net release of carbon to the atmosphere (10^{12} g yr⁻¹) in 1980 from deforestation in the tropics*

	Closed forests	Open forests	Fallow	Total
Mexico	33.1	0.4	0.0	33.4
Costa Rica	6.5	0.0	2.9	9.4
El Salvador	0.2	0.0	0.0	0.2
Guatemala	6.9	0.0	3.1	10.0
Honduras	7.1	0.0	3.1	10.1
Nicaragua	11.8	0.0	5.1	16.9
Panama	3.8	0.0	1.7	5.5
Belize	0.4	0.0	0.2	0.6
Guyana	0.4	0.0	0.0	0.4
Jamaica	0.1	0.0	0.0	0.1
Trinidad & Tobago	0.1	0.0	0.0	0.1
Cuba	0.1	0.0	0.0	0.1
French Guyana	0.3	0.0	0.0	0.3
Haiti	0.1	0.0	0.0	0.1
Dominican Republic	0.1	0.0	0.0	0.1
Surinam	0.4	0.0	0.0	0.4
Bolivia	4.6	0.1	2.0	6.8
Brazil	207.1	39.6	89.4	336.1
Roraima	0.5	0.0	0.2	0.7
Amapa	0.5	0.0	0.2	0.7
Amazonas	5.8	0.0	2.5	8.3
Para	90.2	0.0	39.1	129.3
Maranhao	9.2	4.1	3.9	17.2
Acre	17.0	0.0	7.3	24.3
Rondonia	24.3	0.6	10.5	35.4
Mato Grosso	59.1	32.8	25.5	117.4
Goias	0.5	2.1	0.2	2.8
Colombia	85.1	1.4	36.9	123.3
Ecuador	27.8	0.0	12.1	39.9
Paraguay	8.3	0.1	0.0	8.4
Peru	31.4	0.0	13.6	45.0
Venezuela	13.4	4.5	0.0	17.9
Tropical America	449	46	170	665
Chad	0.0	4.2	0.0	4.2
Gambia	0.0	0.2	0.0	0.2
Mali	0.0	2.1	0.0	2.1
Niger	0.0	1.6	0.0	1.6
Senegal	0.0	2.9	0.0	2.9
Upper Volta	0.0	4.2	0.0	4.2
Benin	0.1	2.3	0.1	2.5
Ghana	2.7	2.6	2.4	7.7
Guinea	3.8	1.7	3.3	8.8
Guinea-Bissau	0.5	2.1	0.4	3.0
Ivory Coast	47.0	11.5	42.0	100.5
Liberia	4.1	0.0	3.7	7.8
Nigeria	29.5	3.5	26.5	59.5
Sierra Leone	0.5	0.0	0.4	1.0
Togo	0.2	0.3	0.2	0.7
Angola	2.9	2.6	0.0	5.5
Cameroon	14.0	1.6	0.0	15.6
Central African Republic	1.0	2.6	0.0	3.6
Congo	3.4	0.0	0.0	3.4
Equatorial Guinea	0.3	0.0	0.0	0.3
Gabon	2.2	0.0	0.0	2.2

Table 4 (*continued*)

	Closed forests	Open forests	Fallow	Total
Zaire	26.8	8.2	0.0	35.0
Burundi	0.0	0.0	0.0	0.0
Ethiopia	0.8	7.0	0.0	7.8
Kenya	1.0	0.7	0.0	1.7
Madagascar	12.1	0.2	10.9	23.2
Malawi	0.0	15.7	0.0	15.7
Mozambique	0.3	6.7	0.0	7.0
Rwanda	0.2	0.1	0.0	0.3
Somalia	0.2	0.9	0.0	1.0
Sudan	0.4	26.2	0.0	26.6
Tanzania	0.7	4.2	0.0	4.9
Uganda	0.8	1.4	0.0	2.2
Zambia	2.6	1.6	0.0	4.2
Zimbabwe	0.0	4.2	0.0	4.2
Botswana	0.0	0.7	0.0	0.7
Namibia	0.0	1.0	0.0	1.0
Tropical Africa	158	125	90	373
Bangladesh	0.7	0.0	1.4	2.1
Bhutan	0.3	0.0	0.0	0.3
India	12.3	0.0	20.7	33.0
Nepal	6.9	0.0	0.0	6.9
Pakistan	1.0	0.1	0.0	1.1
Sri Lanka	1.7	0.0	0.0	1.7
Burma	18.9	0.0	32.3	51.2
Thailand	33.0	5.4	56.1	94.5
Brunei	2.7	0.0	0.0	2.7
Indonesia	70.4	1.8	119.7	191.9
Peninsular Malaysia	24.4	0.0	0.0	24.4
Sabah	11.0	0.0	0.0	11.0
Sarawak	14.5	0.0	0.0	14.5
Philippines	21.0	0.0	35.7	56.7
Kampuchea	4.3	0.5	0.0	4.8
Laos	30.2	3.2	51.3	84.7
Vietnam	13.3	0.0	22.8	36.1
Papua New Guinea	3.4	0.1	0.0	3.5
Tropical Asia	270	11	340	621
All tropics	877	182	600	1659

from responding to increased concentrations of CO₂ (Billings et al., 1984; Tissue and Oechel, 1987). Other evidence suggests that plants (Wong, 1979) and ecosystems (Oechel et al., 1984) may sequester carbon in response to increased levels of CO₂ despite nutrient limitation. The interaction of nutrients and CO₂ is not known well enough at present to predict unambiguously the extent to which natural systems will respond to increased concentrations of CO₂ in air (Strain, 1985).

Another possibility for an increased storage of carbon in the biota and soils (including marine

sediments) is through eutrophication of the biosphere with nitrogen and phosphorus. Based on an element-matching approach, however, this possibility does not seem likely to account for a storage of more than 0.2×10^{15} g C yr⁻¹ (Peterson and Melillo, 1985).

Finally, there is the possibility that climate has been changing in a way that increases the storage of carbon on land or in the oceans. It is presently unclear how the storage of carbon on land is affected in the short term (year to year) by changes in temperature. Some arguments predict an increased storage of carbon with a global

warming (Miller, 1981; Miller et al., 1983); others predict an increased release (Billings et al., 1982, 1983; Schleser, 1982; Woodwell, 1983). The effect of changes in moisture is even more difficult to predict, although recent studies with microcosms from the tundra show that changes in nutrients and depth of water table affect the storage of carbon more than changes in the concentration of atmospheric CO_2 do (Billings et al., 1982, 1983, 1984). The climatic effects of a doubled CO_2 concentration in the arctic tundra are expected to include a rise in summer temperatures from 4° to 8° , a lowering of the water table from increased evapotranspiration, and an increased availability of nutrients as a consequence of increased decomposition of peat. Billings et al. found that lowering the water table from the surface to 10 cm and adding 25 g N m^{-2} had approximately equal effects. The treatments reversed the direction of CO_2 flux from a net storage of about $150 \text{ g CO}_2 \text{ m}^{-2} \text{ season}^{-1}$ to a net release of $300\text{--}400 \text{ g CO}_2 \text{ m}^{-2} \text{ season}^{-1}$ (Billings et al., 1983, 1984). The expected increase in temperature reduced the net storage but did not reverse the direction of flux. The effect of doubling the ambient CO_2 concentration from 400 to 800 ppm had an effect of about the same magnitude, but in the opposite direction, as the doubling of temperature. Doubling the CO_2 concentration and doubling summer temperature increased and decreased, respectively, the net storage of carbon by an average of about $125\text{--}150 \text{ g CO}_2 \text{ m}^{-2} \text{ season}^{-1}$ (Billings et al., 1982, 1983, 1984). Extrapolation of these results to predictions of future fluxes of carbon is tenuous because of the interaction between various of the environmental variables considered. Neverthe-

less, the ecological changes expected to accompany climatic change may change the net annual storage of $0.2 \times 10^{15} \text{ g C}$ in the arctic tundra to a net release of the same magnitude or more.

If there is currently a net storage of carbon on land that balances the net release generated from the direct effects of man, the annual storage is so small in comparison to the pools of carbon in vegetation and soil that it would be undetectable for decades. At present the mechanism of such a change in storage is unclear. Thus, even if the terms of the global carbon equation appeared to balance at present, current information is insufficient to balance them once climatic change becomes important (Houghton and Woodwell, 1983). The direction and magnitude of the biotic flux in response to climate are among the most critical questions for the global carbon cycle and the earth's climate. The effect of climate on the biota could have either a positive or negative feedback on the interaction of CO_2 and global temperature.

4. Acknowledgements

The authors are indebted to Inez Fung for providing the map for Figure 2 and to C. D. Keeling and two anonymous reviewers for helpful comments on the manuscript. The research was sponsored in part by the National Science Foundation (BSR-8110477) and in part by the Carbon Dioxide Research Division, Office of Energy Research, US Department of Energy, under contract number DE-AC05-84OR21400 with Martin Marietta Energy Systems, Inc.

5. Appendices

Appendix 1. Data used to model changes in the carbon in vegetation and soils during harvest and regrowth of forests. Data on USSR forests are from Melillo (1985, pers. comm.). Data on other temperate and boreal forests are from Houghton et al. (1983) with a revised loss of carbon from soils.

	Temperate forest USSR	Boreal forest USSR	Temperate evergreen forest	Temperate deciduous forest	Boreal forest
Carbon in vegetation (10^3 kg/ha)					
1° forest	135	90	160	135	90
2° forest	108	72	120	100	68
Carbon in wood harvested (10^3 kg/ha)	40 (30)*	50 (35)*	30	30	12
Carbon in live vegetation left on site at time of harvest (10^3 kg/ha)					
1° forest	0 (97)*	0 (46)*	0	0	0
2° forest	0 (70)*	0 (28)*	0	0	0
Carbon in dead plant material (slash) left on site at time of harvest (10^3 kg/ha)					
1° forest	95 (8)*	40 (9)*	130	105	78
2° forest	68 (8)*	22 (9)*	90	70	56
<i>k</i> -value for exponential decay of slash	0.08	0.04	—	—	—
Time required for forest to grow before harvested again (years)					
1° forest	40 (4)*	80 (29)*	50	50	50
2° forest	40 (14)*	80 (49)*			
Carbon in soils (10^3 kg/ha)					
1° forest	134	206	134	134	206
2° forest	134	206	120	120	185
Minimum carbon content in soil following harvest (10^3 kg/ha)	134	206	107.2	107.2	164.8
Time required for soil carbon to reach minimum following harvest (years)	—	—	10	10	15
Time required for soil carbon to go from minimum level to level of secondary forest (years)	—	—	40	40	35

* First value is for harvest of industrial wood; value in parentheses is for harvest of non-industrial wood (largely fuelwood).

Appendix 2. Data used to model changes in the carbon in vegetation and soils during the transformation of a natural ecosystem to agriculture, during cultivation, and following abandonment. Values unique to the analysis of the USSR are shown in parentheses.

	Temperate evergreen forest	Temperate deciduous forest	Boreal forest	Temperate woodland shrubland	Temperate grassland
Carbon in vegetation (10^3 kg/ha)					
undisturbed ecosystems	160	135	90	27 (10)	7 (10)
"recovered" ecosystems	120	100 (108)	68 (72)	27 (10)	7 (10)
Carbon in crops (10^3 kg/ha)	5	5	5	5	3 (5)
Time required for an abandoned system to "recover" (years)	50	50 (40)	50 (80)	50	10
Carbon in soils (10^3 kg/ha)					
undisturbed ecosystems	134	134	206	69 (189)	189
"recovered" ecosystems	120	120 (134)	185 (206)	69 (189)	189
Fraction of carbon in vegetation left dead in soil at time of clearing	0.33	0.33 (0.20)	0.33 (0.20)	0.50	0.50
<i>k</i> -value for exponential decay of wood		(0.06)	(0.03)	(0.07)	(0.07)
Fraction of carbon in vegetation assigned to decay pools at time of clearing					
1 year	0.40	0.40 (0.60)	0.40 (0.60)	0.40 (0.80)	0.50 (0.80)
10 years	0.20	0.20 (0.30)	0.20 (0.30)	0.10 (0.20)	0.0 (0.20)
100 years	0.07	0.07 (0.10)	0.07 (0.10)	0.0	0.0
Carbon content of soil after initial, rapid change following clearing (10^3 kg/ha)	80	80 (114)	160 (175)	41 (161)	113 (161)
Minimum carbon content of soil in cultivated system (10^3 kg/ha)	100.5	100.5 (107)	154.5 (165)	51.75 (151)	141.75 (151)
Time required for initial, rapid change in soil carbon following clearing (years)	15	15 (10)	50 (15)	15	15
Time required for carbon in soil to reach minimum value during cultivation (years)	30	30	50 (65)	30	30
Time required for soil carbon to reach "recovered" level in an abandoned system (years)	40	40	35 (80)	45	45

Appendix 3. Annual rates of wood harvest in the USSR (10^9 kg C yr⁻¹) (from Blandon, 1983). Rates for intervening years were interpolated linearly.

		Temperate forest		Boreal forest	
		West	East	West	East
Industrial wood	1932	8.52	2.36	30.20	8.35
	1950	12.96	4.64	45.85	16.35
	1960	15.84	5.72	65.65	23.65
	1970	12.92	6.40	64.35	31.85
	1980	10.56	6.56	55.50	34.45
Non-industrial wood (largely fuelwood)	1932	22.14	3.44	31.06	10.30
	1945	13.41	2.46	18.80	7.34
	1950	9.43	1.84	13.24	5.49
	1960	3.72	0.77	5.21	2.30
	1980	2.97	0.69	4.15	2.07

Appendix 4. The fraction of carbon in harvested wood assigned different decay rates in the USSR. All of the 1-year pool decays in 1 year (fuelwood); one hundredth of the 100-year pool decays in 1 year.

	1932	1945	1960	1975	1980
Industrial wood					
1 year	0.34	0.64	0.29	0.18	0.15
100 years	0.66	0.36	0.71	0.82	0.85
Non-industrial wood (largely fuelwood)					
1 year	0.901	0.929	0.75	0.826	0.82
100 years	0.099	0.071	0.25	0.174	0.18

Appendix 5. Total area in cropland in the USSR (10^6 ha). These data were used to calculate the annual rates of conversion of natural systems to cropland and the abandonment of cropland.

		Temperate forest		Boreal forest		Grassland	Woodland and Shrubland
		West	East	West	East		
	1940	45	10	1	0	74	19
	1950	42	10	1	0	72	20
	1953	45	11	1	0	76	24
	1956	49	13	1	0	82	48
	1958	48	14	1	0	82	50
	1965	52	15	1	0	89	52
	1970	51	15	1	0	87	52
	1973	53	15	1	0	89	56
	1977	54	15	1	0	89	58
	1980	53	15	1	0	88	58

Appendix 6. Annual rates of afforestation in the USSR (10^6 ha yr⁻¹). The model interpolated linearly between the dates given.

1925	1950	1970	1980
0.04	0.14	0.07	0.07

Appendix 7. Data used to model changes in the carbon in vegetation and soils as a result of clearing tropical forests for croplands and pasture. For the carbon in vegetation of undisturbed forests, the upper value applies to carbon stocks derived from FAO/UNEP growing stocks (Brown and Lugo, 1984); the lower value (in parentheses) applies to carbon stocks averaged from direct measurements (Brown and Lugo, 1982).

	Tropical America			Tropical Africa			Tropical Asia		
	Moist	Seasonal	Dry	Moist	Seasonal	Dry	Moist	Seasonal	Dry
Carbon in vegetation (10^3 kg/ha)									
Undisturbed forest	73 (176)	66 (158)	27 (27)	140 (210)	70 (160)	15 (90)	135 (250)	90 (150)	40 (60)
Cropland	5	5	5	5	5	5	5	5	5
Pasture	5	5	5	5	5	5	5	5	5
Fraction of carbon in vegetation assigned to decay pools at time of clearing									
Burned in 1 year	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40
$1/10 \text{ yr}^{-1}$	0.27	0.27	0.27	0.27	0.27	0.27	0.27	0.27	0.27
Left to decay on site	0.33	0.33	0.33	0.33	0.33	0.33	0.33	0.33	0.33
<i>k</i> -value for exponential decay of wood	0.5	0.4	0.3	0.5	0.4	0.3	0.5	0.4	0.3
Carbon in soil (10^3 kg/ha)									
Undisturbed forest	100	100	69	100	100	69	120	80	50
Cropland	70	70	48	70	70	48	84	56	35
Pasture	75	75	41	75	75	52	90	60	37
Time for soil carbon to reach minimum value (years)									
Cropland	5	5	5	5	5	5	5	5	5
Pasture	2	2	2	2	2	2	2	2	2

Appendix 8. Data used to model changes in the carbon in vegetation and soils in the cycle of shifting cultivation. Where two values occur, (a) applies to carbon stocks derived from FAO/UNEP growing stocks (Brown and Lugo, 1984); (b) applies to carbon stocks averaged from direct measurements (Brown and Lugo, 1982).

	Tropical America			Tropical Africa			Tropical Asia		
	Moist	Seasonal	Dry	Moist	Seasonal	Dry	Moist	Seasonal	Dry
Carbon in live vegetation (10 ³ kg/ha)									
Mature fallow									
(a)	29	26	11	56	28	6	90	50	35
(b)	70	63	11	84	64	36	90	50	35
At start of fallow cycle									
(a)	6	6	0	14	7	0	15	15	5
(b)	15	15	0	15	15	0	15	15	5
Carbon assigned to decay pools at time of clearing (10³ kg/ha)									
Burned first year									
(a)	5	5	2	11	5	1	26	16	12
(b)	15	13	2	19	13	10	26	16	12
1/10 oxidized yr ⁻¹									
(a)	5	5	3	5	5	3	5	5	3
(b)	5	5	3	5	5	3	5	5	3
1/1000 oxidized yr ⁻¹ (charcoal)									
(a)	1	1	0	2	1	0	4	2	1
(b)	3	2	0	3	2	2	4	2	1
Left to decay on site									
(a)	12	9	6	24	10	2	40	12	14
(b)	32	28	6	42	29	21	40	12	14
<i>k</i> -value for exponential decay of wood	0.5	0.4	0.3	0.5	0.4	0.3	0.5	0.4	0.3
Carbon in soil (10³ kg/ha)									
Mature fallow									
(a)	90	90	62	90	90	62	108	72	45
(b)	75	75	52	75	75	52	90	60	38
At start of fallow cycle									
(a)	75	75	52	75	75	52	90	60	38
(b)	75	75	52	75	75	52	90	60	38
Length of cycle (years)									
(a)	10	13	3	13	13	11	15	15	10
(b)	10	13	3	13	13	11	15	15	10

Appendix 9. Annual rates of deforestation in the tropics derived from the FAO/UNEP study (1981a, b, c). Rates were assumed constant for years 1940–1980, inclusive, except for clearing for shifting cultivation, where rates increased exponentially.

	Tropical America			Tropical Africa			Tropical Asia		
	Moist	Seasonal	Dry	Moist	Seasonal	Dry	Moist	Seasonal	Dry
Forests cleared for permanent cropland (10^6 ha yr ⁻¹)	0.333	1.073	0.516	0.06	0.24	0.91	0.332	0.589	0.169
Forests cleared for permanent pasture (10^6 ha yr ⁻¹)	0.252	0.813	0.392	0.0	0.0	0.0	0.0	0.08	0.0
Forests cleared for shifting cultivation (10^6 ha yr ⁻¹)									
1940	0.337	1.355	0.040	0.882	0.776	2.074	0.528	0.456	0.020
1950	0.337	1.355	0.040	0.882	0.776	2.074	0.528	0.456	0.020
1980	1.017	3.230	0.834	1.894	1.666	5.059	1.188	1.543	0.068
Fraction of area cleared annually for shifting cultivation from mature fallow	0.67	0.67	0.67	0.70	0.70	0.70	0.67	0.67	0.67
undisturbed forest	0.33	0.33	0.33	0.30	0.30	0.30	0.33	0.33	0.33

Appendix 10. Annual rates of deforestation in the tropics derived from data of Myers (1980, 1984). Rates were assumed constant for years 1940–1980, inclusive, except for clearing for shifting cultivation, where rates increased exponentially.

	Tropical America			Tropical Africa			Tropical Asia		
	Moist	Seasonal	Dry	Moist	Seasonal	Dry	Moist	Seasonal	Dry
Forests cleared for permanent cropland (10^6 ha yr ⁻¹)	0.0	0.0	0.516	0.0	0.0	0.91	0.0	0.0	0.169
Forests cleared for permanent pasture (10^6 ha yr ⁻¹)	0.213	0.687	0.392	0.0	0.0	0.0	0.0	0.0	0.0
Forests cleared for shifting cultivation (10^6 ha yr ⁻¹)									
1940	0.236	1.063	0.040	0.565	0.677	2.074	1.141	1.121	0.020
1980	1.195	3.805	0.834	2.022	2.422	5.559	3.483	5.683	0.068
Fraction of area cleared annually for shifting cultivation from mature fallow	0.67	0.67	0.67	0.64	0.64	0.70	0.64	0.64	0.67
undisturbed forest	0.33	0.33	0.33	0.36	0.36	0.30	0.36	0.36	0.33

Appendix 11. Annual rates of deforestation in the tropics derived from the Production Yearbooks (FAO, 1983). Rates were assumed constant for years 1940–1980.

	Tropical America			Tropical Africa			Tropical Asia		
	Moist	Seasonal	Dry	Moist	Seasonal	Dry	Moist	Seasonal	Dry
Forests cleared for* permanent cropland (10^6 ha yr ⁻¹)	0.681	2.194	1.055	0.153	0.613	2.323	0.272	0.484	0.139
Forests cleared for permanent pasture (10^6 ha yr ⁻¹)	0.251	0.829	0.391	0.0	0.0	0.0	0.0	0.0	0.0
Forests cleared for shifting cultivation (10^6 ha yr ⁻¹)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

* The Production Yearbooks give four general categories of land use: cropland, pasture, forest, and other land. Increases in the area of cropland and pasture do not account for decreases in forest area. Forests are also being replaced by "other land", most likely abandoned agricultural land with lowered fertility that will support neither crops nor forests (Houghton, 1986). In our analysis, we combined changes in other land and in cropland to compute the annual rate of deforestation for croplands.

REFERENCES

- Anuario Estatístico do Brasil. 1979. Volume 40, page 42. Fundação Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.
- Armentano, T. V., Menges, E. S., Molofsky, J. and Lawler, D. J. 1984. Carbon exchange of organic soils ecosystems of the world. Holcomb Research Institute Paper No. 27. Butler University, Indianapolis, Indiana.
- Armentano, T. V. and Ralston, C. W. 1980. The role of temperate zone forests in the global carbon cycle. *Can. J. For. Res.* 10, 53–60.
- Bacastow, R. and Keeling, C. D. 1973. Atmospheric carbon dioxide and radio-carbon in the natural carbon cycle. II. Changes from A.D. 1700 to 2070 as deduced from a geochemical model. In *Carbon and the biosphere* (eds. G. M. Woodwell and E. V. Pecan), US Atomic Energy Commission, Washington, DC, USA., 86–135.
- Bach, W. 1985. Forest dieback: Extent of damages and control strategies. *Experientia* 41, 1095–1104.
- Billings, W. D., Luken, J. O., Mortensen, D. A. and Peterson, K. M. 1982. Arctic tundra: a source or sink for atmospheric carbon dioxide in a changing environment? *Oecologia* 53, 7–11.
- Billings, W. D., Luken, J. O., Mortensen, D. A. and Peterson, K. M. 1983. Increasing atmospheric carbon dioxide: Possible effects on arctic tundra. *Oecologia* 58, 286–289.
- Billings, W. D., Peterson, K. M., Luken, J. O. and Mortensen, D. A. 1984. Interaction of increasing atmospheric carbon dioxide and soil nitrogen on the carbon balance of tundra microcosms. *Oecologia* 65, 26–29.
- Blandon, P. 1983. *Soviet forest industries* (Replica Edition Series). Westview Press, Boulder, Colorado.
- Broecker, W. S., Takahashi, T., Simpson, H. H. and Peng, T.-H. 1979. Fate of fossil fuel carbon dioxide and the global carbon budget. *Science* 206, 409–418.
- Brown, S. and Lugo, A. E. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 14, 161–187.
- Brown, S. and Lugo, A. E. 1984. Biomass of tropical forests: A new estimate based on volumes. *Science* 223, 1290–1293.
- Detwiler, R. P., Hall, C. A. S. and Bodgonoff, P. 1985. Land use change and carbon exchange in the tropics. II. Estimates for the entire region. *Environ. Manage.* 9, 335–344.
- FAO. 1983. *Production Yearbook*. FAO, Rome.
- FAO/UNEP. 1981a. *Tropical Forest Resources Assessment Project. Forest Resources of Tropical Asia*. FAO, Rome.
- FAO/UNEP. 1981b. *Tropical Forest Resources Assessment Project. Forest Resources of Tropical America*. FAO, Rome.
- FAO/UNEP. 1981c. *Tropical Forest Resources Assessment Project. Forest Resources of Tropical Africa*. FAO, Rome.
- Fearnside, P. M. 1984. A floresta vai acabar? *Cienc. Hoje* 2, 42–52.
- Fung, I., Prentice, K., Matthews, E., Lerner, J. and Russell, G. 1983. Three-dimensional tracer study of atmospheric CO₂: Response to seasonal exchanges with the terrestrial biosphere. *J. Geophys. Res.* 88, 1281–1294.
- Gifford, R. M. 1980. Carbon storage by the biosphere. In *Carbon dioxide and climate: Australian research* (ed. G. I. Pearman). Australian Academy of Science, Canberra. 167–181.

- Houghton, R. A. 1986. Estimating changes in the carbon content of terrestrial ecosystems from historical data. In *The changing carbon cycle: a global analysis* (eds. J. R. Trabalka and D. E. Reichle). New York: Springer-Verlag. In press.
- Houghton, R. A., Boone, R. D., Melillo, J. M., Palm, C. A., Woodwell, G. M., Myers, N., Moore, B. and Skole, D. L. 1985a. Net flux of CO₂ from tropical forests in 1980. *Nature* 316, 617–620.
- Houghton, R. A., Hobbie, J. E., Melillo, J. M., Moore, B., Peterson, B. J., Shaver, G. R. and Woodwell, G. M. 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: A net release of CO₂ to the atmosphere. *Ecolog. Monogr.* 53, 235–262.
- Houghton, R. A., Schlesinger, W. H., Brown, S. and Richards, J. F. 1985b. Carbon dioxide exchange between the atmosphere and terrestrial ecosystems. In *Atmospheric Carbon Dioxide and the Global Carbon Cycle* (ed. J. R. Trabalka). Department of Energy, DOE/ER-2039, Washington, DC. 113–140.
- Houghton, R. A. and Woodwell, G. M. 1983. Effect of increased C, N, P and S on the global storage of C. In *The Major Biogeochemical Cycles and their Interactions*. SCOPE 21 (eds. B. Bolin and R. B. Cook). New York: John Wiley and Sons. 327–343.
- IBDF. 1983. Desenvolvimento Florestal no Brasil. Instituto Brasileiro de Desenvolvimento Florestal, Ministeria da Agricultura. Folha Informativa, No. 5.
- Johnson, W. C. and Sharpe, D. M. 1983. The ratio of total to merchantable forest biomass and application to the global carbon budget. *Can. J. For. Res.* 13, 372–383.
- Lemon, E. R. (editor). 1983. *CO₂ and Plants. The response of plants to rising levels of atmospheric carbon dioxide*. AAAS Selected Symposium 84. Westview Press, Inc. Boulder, Colorado.
- Miller, P. C. (editor). 1981. Carbon balance in northern ecosystems and the potential effect of carbon dioxide induced climatic change. US Department of Energy CONF-8003118. National Technical Information Service, Washington, DC. 109 pp.
- Miller, P. C., Kendall, R. and Oechel, W. C. 1983. Simulating carbon accumulation in northern ecosystems. *Simulation* 40, 119–131.
- Molofsky, J., Menges, E. S., Hall, C. A. S., Armentano, T. V. and Ault, K. A. 1984. The effects of land use alteration on tropical carbon exchange. In *The biosphere: problems and solutions* (ed. T. N. Veziroglu). Amsterdam: Elsevier Science Publishers B.V. 181–194.
- Moore, B., Boone, R. D., Hobbie, J. E., Houghton, R. A., Melillo, J. M., Peterson, B. J., Shaver, G. R., Vorosmarty, C. J. and Woodwell, G. M. 1981. A simple model for analysis of the role of terrestrial ecosystems in the global carbon cycle. In *Modelling the Global Carbon Budget*. SCOPE 16 (ed. B. Bolin). New York: John Wiley and Sons. 365–385.
- Myers, N. 1980. *Conversion of tropical moist forests*. National Academy of Sciences Press, Washington, DC.
- Myers, N. 1984. *The primary source*. New York: W. W. Norton & Co.
- Oechel, W. C., Hastings, S., Hilbert, D., Lawrence, W., Prudhomme, T. I., Riechers, G. and Tissue, D. 1984. Response of vegetation to carbon dioxide (Report 019). US Department of Energy, Washington, DC.
- Oechel, W. C. and Strain, B. R. 1985. Native species responses to increased atmospheric carbon dioxide concentration. In *Direct effects of increasing carbon dioxide on vegetation* (eds. B. R. Strain and J. D. Cure). DOE/ER-0238. US Department of Energy, Washington, DC. 117–154.
- Oeschger, H. U., Siegenthaler, U., Schotterer, U. and Gugelmann, A. 1975. A box diffusion model to study the carbon dioxide exchange in nature. *Tellus* 27, 168–192.
- Palm, C. A., Houghton, R. A., Melillo, J. M. and Skole, D. L. 1986. Atmospheric carbon dioxide from deforestation in Southeast Asia. *Biotropics*, in press.
- Pearman, G. I. and Hyson, P. 1980. Activities of the global biosphere as reflected in atmospheric CO₂ records. *J. Geophys. Res.* 85, 4457–4467.
- Peterson, B. J. and Melillo, J. M. 1985. The potential storage of carbon caused by eutrophication of the biosphere. *Tellus* 37B, 117–127.
- Schleser, G. H. 1982. The response of CO₂ evolution from soils to global temperature changes. *Zeitschr. Naturforsch.* 37a: 2037/1–2037/5.
- Schlesinger, W. H. 1986. Changes in soil carbon storage and associated properties with disturbance and recovery. In *The changing carbon cycle: a global analysis* (eds. J. R. Trabalka and D. E. Reichle). New York: Springer-Verlag. In press.
- Strain, B. R. 1985. Physiological and ecological controls on carbon sequestering in ecosystems. *Biogeochem.* 1, 219–232.
- Tardin, A. T., Lee, D. C. L., Santos, R. J. R., de Assis, O. R., dos Santos Barbosa, M. P., de Lourdes Moreira, M., Pereira, M. T., Silva, D. and dos Santos Filho, C. P. 1980. Subprojeto Desmatamento, Convenio IBDF/CNPq-INPE, 1979. (Instituto Nacional de Pesquisas Espaciais, Relatorio No. INPE-1649-RPE/103 Sao Jose Dos Campos, Sao Paulo, 1980).
- Tissue, D. T. and Oechel, W. C. 1987. Physiological and growth response of *Eriophorum vaginatum* to field elevated CO₂ and temperature in the Alaskan tussock tundra. *Ecology*, in press.
- Wong, S. C. 1979. Elevated atmospheric partial pressure of CO₂ and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C₃ and C₄ plants. *Oecologia* 44, 68–74.
- Woodwell, G. M. 1983. Biotic effects on the concentration of atmospheric carbon dioxide: A

- review and projection. In *Changing climate*. National Academy Press, Washington, DC, USA. 216–241.
- Woodwell, G. M., Whittaker, R. H., Reiners, W. A., Likens, G. E., Delwiche, C. C. and Botkin, D. B. 1978. The biota and the world carbon budget. *Science* 199, 141–146.