Balancing the Global Carbon Budget

R.A. Houghton

The Woods Hole Research Center, Falmouth, Massachusetts 02540;
email: rhoughton@whrc.org

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carbon sinks, climate feedbacks, CO_2, fossil fuels, oceans, terrestrial ecosystems

Abstract

The global carbon budget is, of course, balanced. The conservation of carbon and the first law of thermodynamics are intact. "Balancing the carbon budget" refers to the state of the science in evaluating the terms of the global carbon equation. The annual increases in the amount of carbon in the atmosphere, oceans, and land should balance the emissions of carbon from fossil fuels and deforestation. Balancing the carbon budget is not the real issue, however. The real issue is understanding the processes responsible for net sources and sinks of carbon. Such understanding should lead to more accurate predictions of future concentrations of CO_2 and more accurate predictions of the rate and extent of climatic change. The recent past may be insufficient for prediction, however. Oceanic and terrestrial sinks that have lessened the rate of growth in atmospheric CO_2 until now may diminish as feedbacks between the carbon cycle and climate become more prominent.

1. INTRODUCTION

As of June 1, 2006, 189 nations, including the United States, adopted the United Nations Framework Convention on Climate Change (UNFCCC), which has as its objective "stabilization of greenhouse gas concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system." The global carbon cycle is critical to this objective because its processes define how emissions of carbon dioxide (CO_2) from anthropogenic activity translate into concentrations of CO_2 in the atmosphere. How much of the carbon emitted to the atmosphere remains there, and how much of the emissions are taken up by terrestrial ecosystems and by the world's oceans? Answers to these questions will provide at least a part of the scientific understanding necessary for establishing the amount and rate of CO_2 emissions that would meet a "safe" concentration.

Feedbacks between the carbon cycle and the climate system are critical for projecting changes in climate. For example, if the warming leads to enhanced rates of decay of organic matter in soils, or a reduction in oceanic carbon uptake, then the concentration of CO_2 in the atmosphere will rise more rapidly than it would in the absence of such (positive) feedbacks, and the rate of warming will be greater as well. Conversely, if increased CO_2 in the atmosphere enhances photosynthesis and the storage of carbon in plants and soils, then CO_2 levels will rise less rapidly than in the absence of this (negative) feedback, and climate change will also be slower as a result. There are physical feedbacks such as the effects of clouds on Earth's radiation balance, although many of these are already incorporated in the general circulation models (GCMs) used to predict climate change. In contrast, feedbacks between the carbon cycle and climate have not been included in GCMs until very recently with the development of coupled climate and carbon cycle models.

Carbon dioxide is, by far, the largest contributor to the anthropogenically enhanced greenhouse effect and is likely to remain so in the future. The importance of CO_2 to the climate has provided the impetus for research on the global carbon cycle. The global carbon cycle refers to the exchanges of carbon within and between four major reservoirs: the atmosphere, the oceans, land, and fossil fuels. The exchanges may occur in seconds (for example, the fixation of atmospheric CO_2 into sugar through photosynthesis) or over millennia [for example, the accumulation of fossil carbon (coal, oil, gas) through deposition and diagenesis of organic matter]. The emphasis of this review is on the exchanges that are important over years to a few centuries.

This review first addresses the reservoirs and background flows of carbon in the global carbon system. Then I review the sources of carbon to the atmosphere from fossil fuels and land-use change and the sinks of carbon on land and in the oceans that have modulated the accumulation of CO_2 in the atmosphere on short timescales (1–100 years). After a review of the mechanisms that transfer carbon between the atmosphere and terrestrial and oceanic reservoirs, the review evaluates whether these sinks can accommodate the increased emissions from fossil fuels and implications for the future.

The review focuses on two outstanding questions that have concerned scientists investigating the global carbon cycle since the first carbon budgets were constructed

in the late 1960s (SCEP 1970): How much of the carbon released to the atmosphere from combustion of fossil fuels and changes in land use is taken up by the oceans and by terrestrial ecosystems? And, What are the mechanisms responsible for the uptake of carbon? The mechanisms controlling carbon sinks are important because different mechanisms have different implications for the rate at which CO_2 will increase in the future, and ultimately on the rate of global warming.

Many reviews of the carbon cycle have appeared in the past 30 years. The most recent and comprehensive of them, particularly with respect to climate, are those prepared by the Intergovernmental Panel on Climate Change (IPCC) (Watson et al. 1990, Schimel et al. 1996, Prentice et al. 2001). The fourth IPCC assessment will appear in 2007. The basic aspects of the global carbon cycle have been understood for ~35 years, but predictions of how sources and sinks of carbon will respond to a changing climate are actively debated.

2. MAJOR RESERVOIRS AND BACKGROUND FLUXES OF CARBON

2.1. Reservoirs

The contemporary global carbon cycle is shown in simplified form in **Figure 1**. The four major reservoirs important in the time frame of years to centuries are the atmosphere, oceans, reserves of fossil fuels, and terrestrial ecosystems, including vegetation and soils. Over millennia, processes such as weathering, vulcanism, seafloor spreading, and diagenesis are dominant, but the amounts of carbon exchanged annually through these processes are small and generally ignored in budgets of a century or so (see Sundquist & Visser 2004 for a recent review of the carbon cycle over longer time frames).

2.1.1. The atmosphere. In 2005 the globally averaged concentration of CO_2 was nearly 0.0380%, or 380 ppmv (parts per million by volume), equivalent to approximately 805 PgC (1 Pg = 1 petagram = 10^{15} g = 10^9 metric tonnes). Methane (~1.7 ppm), carbon monoxide (~0.1 ppm), and nonmethane hydrocarbons are other carbon-containing gases important either directly or indirectly in Earth's radiative balance. From the perspective of the global carbon balance (not climate), however, these other gases may be ignored.

2.1.2. The oceans. The total amount of carbon in the world's oceans is approximately 38,000 PgC, nearly 50 times more carbon than in the atmosphere. Most of this oceanic carbon is in intermediate and deep waters; only 700–1000 PgC are in the surface ocean in direct contact with the atmosphere. There are also 6000 PgC of reactive carbon within ocean sediments, which, although important in determining the long-term concentration of CO_2 in the atmosphere and oceans, are less important as a part of the short-term carbon cycle.

Most gases are not very soluble in water and, thus, are predominantly in the atmosphere. Only approximately 1% of the world's oxygen, for example, is in the oceans;

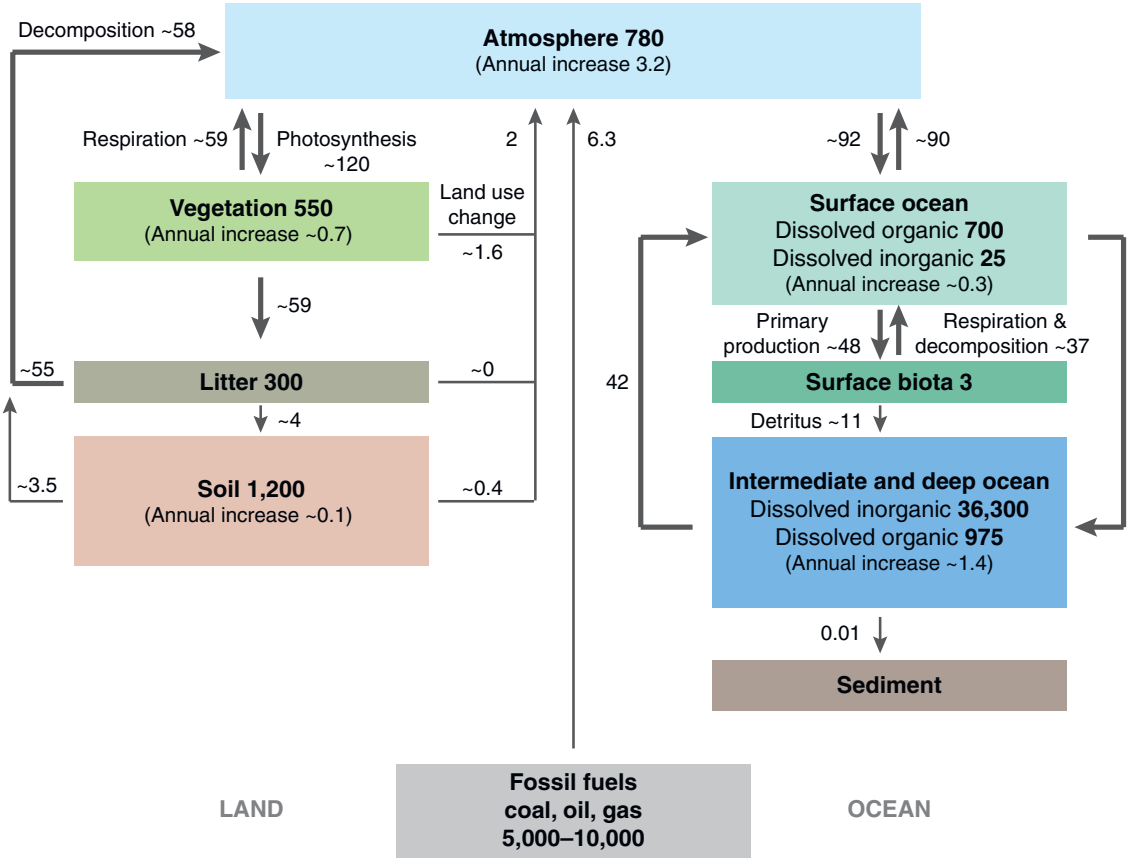

Figure 1

The global carbon cycle in the 1990s. Units are PgC or PgC year^{-1}.

99% exists in the atmosphere. Because of the chemistry of seawater, however, the distribution of carbon between air and sea is reversed: 98.5% of the carbon in the ocean-atmosphere systems is in the sea. Nearly all of this carbon exists as dissolved inorganic carbon (DIC), and most of the DIC is in the form of bicarbonate and carbonate ions. Less than 1% of the DIC is in the form of dissolved CO_2 (pCO_2) (Sarmiento 1993). Approximately 1000 PgC of the DIC are organic, mostly in dissolved form, and only approximately 3 PgC are in living organisms.

2.1.3. Terrestrial ecosystems: vegetation and soils. Carbon accounts for approximately 0.27% of the mass of elements in Earth's crust (Kempe 1979), yet accounts for approximately 50% of dry (water removed) organic matter. The amount of carbon contained in terrestrial vegetation (550 ± 100 Pg) is on the order of the amount in the atmosphere (800 Pg). The organic matter in soils is two to three times this amount [1500–2000 PgC in the top meter and as much as 2300 Pg in the top

3 m (Jobággy & Jackson 2000)]. Forests are particularly important as a carbon reservoir because trees hold much more carbon per unit area than other types of vegetation.

2.1.4. Fossil fuels. Coal, oil, and natural gas are the residuals of organic matter formed millions of years ago by green plants. The amount of carbon stored in recoverable reserves of coal, oil, and gas is estimated to be 5000–10,000 PgC, larger than any other reservoir except the deep sea, and about ten times the carbon content of the atmosphere.

2.2. Background Flows of Carbon

The redistribution of fossil carbon (from fossil fuels) among the atmosphere, oceans, and land dominates the global carbon budget today. Natural flows of carbon can no longer be discerned because the reservoirs and fluxes in the active carbon cycle are so altered as a result of this redistribution of fossil carbon over the past few centuries. Even obviously natural processes, such as photosynthesis, which may be readily distinguished from human-induced processes, are nonetheless impacted by carbon fluxes resulting from the burning of fossil fuels.

The pre-anthropogenic fluxes of carbon between the oceans and the atmosphere are approximately 90 PgC $year^{-1}$ in each direction (**Figure 1**). These gross fluxes are largely the result of diffusion across the air-sea interface, although ocean circulation, carbon chemistry, and biology are also important. Primary productivity in the world oceans is estimated to be approximately 48 PgC $year^{-1}$ (Longhurst et al. 1995). Approximately 25% of this production sinks from the photic zone to deeper water (Falkowski et al. 1998, Laws et al. 2000). The flux of carbon from the surface ocean to the intermediate and deep ocean is estimated to be approximately 40 Pg per year, in part from the sinking of organic production (11 PgC $year^{-1}$) and in part from vertical mixing (33 PgC $year^{-1}$), which also returns 42 PgC $year^{-1}$ back to the surface.

The background exchanges of carbon between terrestrial ecosystems and the atmosphere are largely the result of biological processes: photosynthesis and respiration ($\sim$120 PgC $year^{-1}$ in each direction). Year-to-year variations in these fluxes owing to climatic variations, including variations in fires, may be as high as 5 PgC $year^{-1}$ (Peylin et al. 2005).

3. CHANGES IN THE CARBON CYCLE AS A RESULT OF HUMAN ACTIVITIES

3.1. Changes Over the Period 1850–2005

Scientists have used a combination of data and models to reconstruct changes in the global carbon cycle over the past centuries. The historical information includes rates of fossil fuel use, rates of land-use change, and past CO_2 concentrations obtained from ice cores.

3.1.1. Emissions of carbon from combustion of fossil fuels. The CO_2 released annually from the combustion of fossil fuels (coal, oil, and gas, including emissions from the production of cement and gas flaring) has increased nearly exponentially over the past 250 years, with temporary interruptions in the trend during the two World Wars, following the increase in oil prices in 1973 and 1979, and following the collapse of the former Soviet Union in 1992. Approximately 300 PgC have been released since 1750, essentially all of it since 1860. Estimates are thought to be known globally to within 20% before 1950 and to within 6% since 1950 (Keeling 1973, Andres et al. 1999).

3.1.2. The increase in atmospheric carbon dioxide. In 2005, the concentration of atmospheric CO_2 reached nearly 380 ppm, an increase of ~35% above the pre-industrial concentration of CO_2 in the atmosphere (275–285 ppm). The average rate of increase in the concentration has been approximately 1 ppm $year^{-1}$ (~2 PgC $year^{-1}$) since 1958 when Charles D. Keeling began the first systematic monitoring of CO_2 concentrations at Mauna Loa, Hawaii, and at the South Pole (Keeling et al. 2001), and the annual increase is accelerating (**Figure 2**). Today there are approximately 100 stations worldwide where weekly flask samples of air are collected, analyzed for CO_2 and other constituents, and where the resulting data are integrated into a consistent global data set (Masarie and Tans 1995).

The increasing concentration of CO_2 in the atmosphere is attributable to human activities, and fossil fuel burning in particular, for several reasons. First, the known sources of carbon are more than adequate to explain the observed increase in the

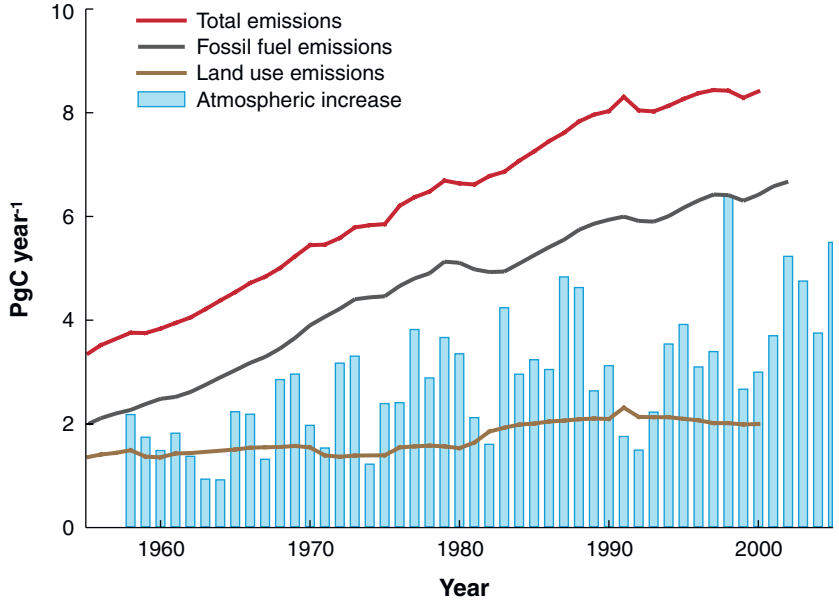

Figure 2

Annual emissions of carbon from the combustion of fossil fuels and from changes in land use, and the annual increase in atmospheric CO_2 (in PgC) over the period 1958 to 2005.

atmosphere. Balancing the global carbon budget requires additional carbon sinks, not an unexplained source of carbon (Section 3.1.4).

Second, for thousands of years preceding 1850 (approximately the start of the industrial revolution), the concentration of CO_2 varied between 260 and 280 ppm (Monnin et al. 2001). Since 1850, concentrations have increased by ~35%. The timing of the increase is coincident with the rising emissions of carbon from fossil fuel combustion and land-use change.

Third, the latitudinal gradient in CO_2 concentrations is highest at northern mid-latitudes and lower at higher and lower latitudes, consistent with the fact that most of the emissions of fossil fuel are located in northern mid-latitudes. This latitudinal gradient has increased in proportion to emissions of carbon from fossil fuels (Keeling et al. 2005).

Finally, the rate of increase of carbon in the atmosphere and the distribution of carbon isotopes and other biogeochemical tracers are consistent with scientific understanding of the sources and sinks of carbon from fossil fuels, land, and the oceans. For example, the increase in concentrations over the period 1850 to 2000 was accompanied by a decrease in the ^{14}C content of CO_2. The decrease is what would be expected if the CO_2 added to the system were fossil carbon depleted in ^{14}C through radioactive decay. This dilution of $^{14}CO_2$ is called the Suess effect.

The concentration of methane has also increased over the past two centuries by more than 100%, from background levels of less than 0.8 ppm to a value of approximately 1.75 ppm in 2000 (Prather & Ehhalt 2001). The temporal pattern of the increase is similar to that of CO_2.

3.1.3. Uptake of CO_2 by the oceans. A comprehensive survey of the distribution of inorganic carbon in the global oceans, carried out in the 1990s by two international ocean research programs, the World Ocean Circulation Experiment (WOCE) and the Joint Global Ocean Flux Study (JGOSFS), provided data for estimating the amount of anthropogenic carbon that has accumulated in the oceans. Using an ocean tracer-based method (Gruber et al. 1996) to separate anthropogenic CO_2 from measured DIC concentrations, a recent analysis (Sabine et al. 2004) calculated a cumulative oceanic sink of 118 ± 19 PgC for the period 1800–1994 (~48% of the total fossil fuel emissions over that period).

3.1.4. Changes in carbon storage on land. Two approaches have been used to calculate changes in terrestrial carbon storage over the past 150 years. The results from the two approaches are so different that they imply that two distinctly different processes have been affecting terrestrial ecosystems.

3.1.4.1. Net exchange of carbon between terrestrial ecosystems and the atmosphere. One estimate of the change in terrestrial carbon over the past 200 years is obtained by difference; that is, by the changes in the other three reservoirs (**Table 1**). According to this method, the world's terrestrial ecosystems were a net source of 38 (±28) PgC to the atmosphere over the period 1800–1994. Total emissions to the atmosphere were, thus, 283 PgC (244 ± 20 from fossil fuels and cement production plus 39 ± 28

from land), and the airborne fraction, defined relative to total emissions, was 58% percent.

3.1.4.2. Changes in land use. A more direct approach for determining at least a portion of terrestrial sources and sinks is based on the large changes per hectare in vegetation and soil carbon that result from changes in land use, such as the conversion of forests to agricultural lands (Houghton 2003). The flux of carbon from changes in land use depends on the area of land affected, the carbon stocks before and after change, and the rates of decay and recovery following disturbance or management. Over the past 300 years, forests have been replaced with agricultural lands and, thus, the amount of carbon on land has decreased. Although carbon has accumulated on land in some regions (Houghton et al. 1999, Pacala et al. 2001), the change resulting from direct human activity over the 150-year period from 1850 to 2000 is estimated to have been a release of 156 PgC (Houghton 2003).

3.1.4.3. A residual terrestrial flux of carbon. The amount of carbon calculated to have been released from changes in land use (156 PgC) (Houghton 2003) is much larger than the amount calculated to have been released from consideration of the other terms in the global carbon equation (38 PgC) (Sabine et al. 2004) (**Table 1**). The difference between these two estimates (a residual sink of 118 PgC) may be due to errors in the analyses (either the ocean models or the land-use change calculations), or it may indicate a terrestrial flux of carbon unrelated to land-use change. The release of carbon calculated from changes in land use includes only the sources and sinks of carbon resulting directly from human activity; ecosystems not directly modified by human activity are left out of the analysis. The release computed by difference, in contrast, includes all ecosystems and all processes. It yields a net terrestrial flux of carbon.

Temporal patterns in the net terrestrial flux and the land-use flux are instructive. The net terrestrial flux can be inferred from inverse calculations with ocean carbon models, where variations in atmospheric CO_2 over the past two centuries are used to

Table 1 The global carbon budget for two intervals (units are PgC)

	1800 to 1994	1850–2000
Emissions from fossil fuels and cement production	244 ± 20[1]	275[3]
Atmospheric increase	-165 ± 4[1]	−175[4]
Oceanic uptake	-118 ± 19[1]	−140[5]
Net terrestrial source	39 ± 28[1]	40
Land-use change (source)	174[2]	156[2]
Residual terrestrial sink	−135	−116

[1] Sabine et al. 2004.
[2] Houghton 2003.
[3] Keeling 1973, Andres et al. 1999.
[4] Prentice et al. 2001.
[5] Joos et al. 1999b.

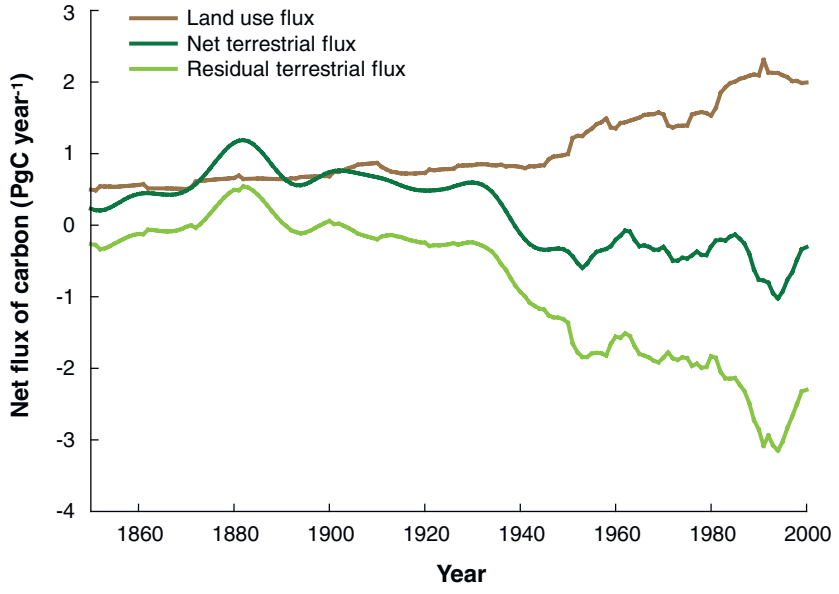

Figure 3

The annual net flux of carbon between terrestrial ecosystems and the atmosphere [from inverse calculations with an ocean carbon model (Joos et al. 1999b, updated)], the flux of carbon from changes in land use (from Houghton 2003), and the difference between them (i.e., the residual terrestrial sink). Positive values indicate a source of carbon to the atmosphere; negative values indicate a terrestrial sink.

calculate annual sources and sinks of carbon on land (by difference) and in the ocean. One such inverse calculation (Joos et al. 1999b) suggests that terrestrial ecosystems were a small net source of carbon until about 1935 and then became a small, variable net sink (**Figure 3**). The historical pattern of this net terrestrial flux is quite different from the pattern of flux attributable to changes in land use. The latter has generally increased over time, whereas the inversion approach suggests that the largest releases of carbon from land were before 1930 and that since 1940 terrestrial ecosystems have been a small net sink. Interestingly, the two estimates (land-use change and net flux from inverse modeling) are similar before approximately 1935. This suggests that the net flux of carbon from terrestrial ecosystems reflects changes in land use up to 1935, and that after this time, the net terrestrial carbon sink is greater than can be accounted for by changes in land use alone. The residual terrestrial flux (the difference between the net terrestrial flux and the land-use flux) was essentially zero before 1935 and has been a negative value (i.e., a carbon sink) since then. By the mid-1990s, this residual sink had grown to ~3 PgC year^{-1}. The location and the mechanisms for this residual sink are uncertain (Section 4.2).

3.2. Changes Over the Period 1980–2000

Since approximately 1980, new types of measurements, longer records of data, and sophisticated methods of analysis have enabled better estimates of the uptake of carbon by the world's oceans and terrestrial ecosystems. The following section addresses the results of these analyses at the global level, with an emphasis on terrestrial ecosystems.

Of the four terms in the global carbon budget, the emissions of carbon from fossil fuels and the growth rate of CO_2 in the atmosphere are well constrained. The

Table 2 The global carbon budget (PgC year^{-1})

	1980s	1990s	2000–2005
Fossil fuel emissions	5.2 ± 0.3	6.4 ± 0.3	7.2 ± 0.3
Atmospheric increase	-2.9 ± 0.1	-3.2 ± 0.2	-4.2 ± 0.1
Oceanic uptake	-1.9 ± 0.6	-2.2 ± 0.7	-2.2 ± 0.4
Net terrestrial flux	-0.4 ± 0.7	-1.0 ± 0.8	-0.8 ± 0.8
Land-use change	1.5 ± 0.8	1.6 ± 0.8	1.5 ± 0.8
Residual terrestrial flux	-1.9 ± 1.1	-2.6 ± 1.1	-2.3 ± 1.1

From Canadell et al. 2007b.

emissions from fossil fuels and cement production have increased steadily from an average of 5.4 (±0.3) PgC year^{-1} during the 1980s, to 6.3 (±0.3) PgC year^{-1} during the 1990s, and to 7.0 (±0.3) PgC year^{-1} over the period 2000–2005 (**Table 2**). The average rate of growth of carbon in the atmosphere was 3.3 (±0.1), 3.2 (±0.1), and 4.1 (±0.1) during these periods, respectively, indicating that 50%–60% of fossil fuel emissions remain airborne.

A number of different approaches are in agreement that the oceans have taken up ~2 PgC year^{-1} over the past two decades (Gurney et al. 2002, Plattner et al. 2002, Sabine et al. 2004, Bender et al. 2005, Miller et al. 2005, Manning & Keeling 2006). The uptake increased slightly from 1.8 (±0.8) in the 1980s, to 2.2 (±0.4) in the 1990s and the first half decade of the twenty-first century (McNeil et al. 2003, Canadell et al. 2007).

Some of the approaches [e.g., the O_2-CO_2 approach (Plattner et al. 2002, Bender et al. 2005, Manning & Keeling 2006)] calculate changes in terrestrial and oceanic carbon storage. Others [e.g., the inverse method (Gurney et al. 2002)] yield fluxes of carbon between the land or ocean surface and the atmosphere. Fluxes are not equivalent to changes in storage. For example, net exchanges with the atmosphere are not equivalent to changes in the pools of C on land or in the sea if some of the carbon fixed by terrestrial plants is transported by rivers to the ocean and respired there. However, when the sources and sinks estimated from inverse calculations are adjusted for carbon transport in rivers, the two approaches based on atmospheric measurements yield similar estimates for the oceanic sink (~2 PgC year^{-1}).

The term in the global carbon budget with the least agreement among estimates is the net terrestrial balance. To balance the carbon budget with the three terms given above, the net terrestrial flux has to have been a sink of 0.4 (±0.7), 1.0 (±0.8), and 0.8 (±0.8) PgC year^{-1} during the 1980s, 1990s, and first five years of the twenty-first century, respectively (**Table 2**).

Land-based or bottom-up approaches used to estimate the terrestrial flux give very different results. For example, deforestation, reforestation, cultivation, and logging were responsible for a release of 2.0 PgC year^{-1} globally during the 1980s and 2.2 PgC year^{-1} during the 1990s (Houghton 2003). Other studies have calculated net fluxes that range from 0.5 to 2.4 PgC year^{-1} (for the tropics) (Fearnside 2000, DeFries et al. 2002, Achard et al. 2004) and 0.8 PgC year^{-1} (for changes in global croplands) (McGuire et al. 2001).

Table 3 Estimates of the annual terrestrial flux of carbon (PgC year^{-1}) in the 1990s according to different methods. Negative values indicate a terrestrial sink

	O_2 and CO_2	Inverse calculations CO_2, $^{13}CO_2$, O_2	Forest inventories	Land-use change
Globe	−0.7 (±0.8)[1]	−0.8 (±0.8)[2]	–	2.2 (±0.6)[3]
Northern mid-latitudes	–	−2.1 (±0.8)[4]	−0.6[5]	−0.03 (±0.5)[3]
Tropics		1.5 (±1.2)[6]	−0.6 (±0.3)[7]	0.5 to 3.0[8]

[1] Plattner et al. 2002.
[2] –1.4 (±0.8) (from Gurney et al. 2002) reduced by 0.6 to account for river transport (Aumont et al. 2001).
[3] Houghton 2003.
[4] –2.4 (from Gurney et al. 2002) reduced by 0.3 to account for river transport (Aumont et al. 2001).
[5] Forests only, including wood products (Goodale et al. 2002).
[6] 1.2 from Gurney et al. (2002) increased by 0.3 to account for river transport (Aumont et al. 2001).
[7] Undisturbed forests (Phillips et al. 1998, Baker et al. 2004).
[8] Fearnside 2000, DeFries et al. 2002, Houghton 2003, Achard et al. 2004.

Despite large variation in the source of carbon attributed to land-use change, all of the estimates are very different from the net terrestrial sink determined from top-down analyses (0.7 PgC year^{-1}) (**Table 3**). Are the methods biased? Biases in the inverse calculations may be in either direction. A stronger rectifier effect (the seasonal covariance between the terrestrial carbon flux and atmospheric transport) generally increases the estimated terrestrial sink (Denning et al. 1995, Gurney et al. 2004). On the other hand, if the near-surface concentrations of atmospheric CO_2 in northern mid-latitude regions are naturally lower than those in the southern hemisphere, the apparent sink in the north may not be anthropogenic, as usually assumed. Rather, the anthropogenic sink would be less than 0.5 PgC year^{-1} (Taylor & Orr 2000). The pre-industrial north-south gradient is unknown.

In contrast to the unknown bias of atmospheric methods, analyses based on land-use change are deliberately biased, as discussed above. These analyses consider only those changes in terrestrial carbon resulting directly from human activity (conversion and modification of terrestrial ecosystems). They do not include sources or sinks of carbon unrelated to land-use change (such as those that might be caused by CO_2 fertilization, changes in climate, or deposition of reactive nitrogen).

If the net terrestrial flux of carbon during the 1990s was a sink of 0.7 PgC year^{-1}, and the amount emitted as a result of changes in land use was 2.2 PgC year^{-1}, then 2.9 PgC year^{-1} must have accumulated on land for reasons not related to land-use change (**Table 3**, **Figure 3**). The range of estimates from analyses of land-use change yields a residual terrestrial flux that ranges between ~1 and ~3 PgC year^{-1}.

4. MECHANISMS RESPONSIBLE FOR CARBON SINKS

4.1. The Oceans

Four processes control the uptake of carbon by the world's oceans: the ocean's carbon chemistry, the air-sea exchange, the mixing between surface and deep waters, and

ocean biology. In the long term (centuries to millennia), the concentration of CO_2 in the atmosphere is controlled by the partial pressure of CO_2 (pCO_2) in the oceans. Because of the ocean's buffer factor, less than 1% of the DIC exists as dissolved CO_2; more than 99% of it exists as bicarbonate and carbonate anions. The chemical equilibrium among these three forms of DIC is responsible for the high solubility of CO_2 in the oceans. But it is also responsible for the fact that the oceans will take up only 80%–85% of the anthropogenic carbon added to the atmosphere (Broecker et al. 1979), not the 98% suggested by comparing reservoir sizes of ocean and atmosphere.

The uptake of carbon by the surface waters is driven by the gradient in pCO_2 between the atmosphere and the surface waters. In contrast to this rapid exchange, the slow process of advection drives the mixing of surface waters with the deeper ocean. This mixing between surface and deeper layers is the bottle-neck for the oceanic uptake of CO_2, and it has enabled the atmosphere to be out of equilibrium with the oceans.

Although the oceanic uptake of CO_2 is dominated in the long term by chemistry and in the short term by vertical mixing, ocean biology is also significant. The biological pump transfers organic matter produced by phytoplankton at the surface to intermediate and deep waters. The net effect of the sinking and decomposition of organic matter is to enrich the deeper waters in CO_2 relative to surface waters and thus to reduce the CO_2 concentration of the atmosphere. The process is estimated to keep the concentration of CO_2 in air approximately 30% of what it would be in its absence (Sarmiento 1993).

These processes are simulated by ocean carbon cycle models and used to predict future as well as past sources and sinks of carbon in the ocean and on land (e.g., Joos et al. 1999b). The models are not always consistent with the distribution of pCO_2 (Lefèvre et al. 2004) or radiocarbon and chlorofluorocarbon-11 in the oceans (Matsumoto et al. 2004), however, suggesting that the current suite of models, although state–of–the art, is not entirely reliable.

4.2. Terrestrial Ecosystems

The mechanisms responsible for carbon sinks on land are not as clear as they are for the oceans; or, perhaps, terrestrial ecologists are not as unified as oceanographers. Two competing mechanisms have been advanced:

- Enhanced growth from physiological or metabolic factors that affect rates of photosynthesis, respiration, growth, and decay
- Regrowth from past disturbances, changes in land use, or management, affecting the mortality of forest stands, the age structure of forests, and hence their rates of carbon accumulation.

Consider, first, enhanced rates of growth.

4.2.1. Physiological or metabolic factors that enhance rates of growth and carbon accumulation. Carbon is taken up from the atmosphere through photosynthesis and released through respiration, including the respiration of plants, animals,

and microbes (largely soil respiration), and fire. An imbalance between these two processes will cause ecosystems to be either sinks or sources of carbon. All things being equal, an increase in productivity will lead to an increase in carbon storage until the carbon lost from the detritus pool comes into a new equilibrium with the higher input of productivity. The longer the turnover time, the greater the disequilibrium or potential increase in storage.

4.2.1.1. CO_2 fertilization. Experiments have shown that most C_3 plants (all trees, many crops, and vegetation from cold regions) respond to elevated concentrations of CO_2 with increased rates of photosynthesis, increased productivity (Norby et al. 2005), and increased biomass. The biomass response to elevated CO_2 averages between 20% and 30% based on measurements from more than 100 experiments (Kimball et al. 1993, Luo et al. 2006), although the increase is not universally observed (Körner et al. 2005). The pools of carbon in litter and soil carbon also increase under elevated CO_2 (Jastrow et al. 2005, Luo et al. 2006).

4.2.1.2. Nitrogen fertilization. Human activity has increased the availability of biologically active forms of nitrogen (NO_x and NH_4), largely through the production of fertilizers, the cultivation of legumes that fix atmospheric nitrogen, and the use of internal combustion engines. Because the availability of N is thought to limit NPP in temperate-zone ecosystems, the addition of N through human activities is expected to increase NPP and, hence, terrestrial carbon storage (Peterson & Melillo 1985, Schimel et al. 1996). Based on the high ratios of C:N in woody tissues, additional N should lead to accumulations of carbon in biomass.

4.2.1.3. Climatic variability and climatic change. Warmer temperatures and changes in soil moisture often favor the growth of trees and, in the longer term, the spread of trees into tundra, savannas, and grasslands. Increased temperatures in cold ecosystems (for example, tundra and taiga) increase productivity and carbon storage [perhaps indirectly, through increased rates of N mineralization (Jarvis & Linder 2000)]. One aspect of warmer temperatures is longer growing seasons, as observed over the boreal zone and temperate Europe (Myneni et al. 1997).

4.2.1.4. Synergies among physiological mechanisms. The factors described above often interact nonadditively to influence carbon storage. For example, higher concentrations of CO_2 enable plants to acquire the same amount of carbon with a smaller loss of water through their stomata. This increased water-use efficiency reduces the effects of drought. Higher levels of CO_2 may also alleviate other stresses of plants, such as high temperatures and ozone. The observation that productivity is increased relatively more in low productivity years suggests that the indirect effects of CO_2 in ameliorating stress may be more important than the direct effects of CO_2 on photosynthesis (Luo et al. 1999).

CO_2 and nutrients may also interact synergistically to increase carbon storage. Nitrogen fertilizer and elevated CO_2, together, had a greater effect on forest growth

than the sum of their individual effects (Oren et al. 2001). The relative stimulation was, again, greater in a nutritionally poor site.

Other experiments have shown a negative synergy. Alone, increases in temperature, precipitation, nitrogen deposition, and atmospheric CO_2 concentration each increased net primary production in a California grassland (Shaw et al. 2003). When the treatments were combined, however, elevated CO_2 decreased the positive effects of the other treatments. That is, elevated CO_2 increased productivity under poor growing conditions, but reduced it under favorable growing conditions. The most likely explanation is that some soil nutrient became limiting, either because of increased microbial uptake or decreased root allocation (Shaw et al. 2003).

An important message from these results is that it is exceedingly difficult, if not impossible, to attribute terrestrial carbon sinks to individual, or combinations of, environmental factors influencing physiology or metabolism.

4.2.2. Demographic or disturbance mechanisms. Terrestrial sinks also result from the recovery (growth) of ecosystems disturbed in the past. The processes responsible for regrowth include physiological and metabolic processes, but they also involve more integrated processes, such as succession, growth, mortality, and aging. Stand-level disturbances initiate regrowth, and forests accumulate carbon as they grow. Climate affects terrestrial carbon storage not only through physiological or metabolic effects on plant growth and respiration, but also through effects on stand demography in response, for example, to mortality and recovery from droughts, storms, or fires.

Until a few years ago, the most common explanations for the residual terrestrial carbon sink were factors that affect the physiology of plants and microbes: CO_2 fertilization, N deposition, and climatic variability. Several recent findings have started to shift the explanation to include management practices and disturbances that affect the age structure or demography of ecosystems. For example, CO_2 fertilization may be less important in forests than in short-term greenhouse experiments (Oren et al. 2001). Secondly, physiological models quantifying the effects of CO_2 fertilization and climate change on the growth of U.S. forests could account for only a small fraction of the carbon accumulation observed in those forests (Schimel et al. 2000). The authors acknowledged that past changes in land use were likely to have been important. Thirdly, and most importantly, 98% of the recent accumulations of carbon in U.S. trees could be explained by the age structure of trees without requiring growth enhancement (Caspersen et al. 2000). Either the physiological effects of CO_2, N, and climate have been unimportant or their effects have been offset by other influences. And finally, the recent estimates of sinks in the United States (Houghton et al. 1999, Pacala et al. 2001) are explained to a large extent on changes in land use and management, and not on physiological models of plant and soil metabolism.

To date, investigations of these two different classes of mechanisms have been largely independent. The effects of changing environmental conditions have been ignored in analyses of land-use change, and physiological models have generally ignored changes in land use.

4.3. Regional Carbon Budgets

Insights into the magnitude of carbon sources and sinks and the mechanisms responsible for sinks may be obtained from a consideration of tropical and extra-tropical regions, separately.

4.3.1. The northern mid-latitudes. The carbon sink in northern mid-latitudes has been estimated by three independent methods and agreement is poor. The global terrestrial sink of ~0.7 PgC year^{-1} determined by inverse methods in the mid-1990s was not evenly distributed by latitude. Net sinks of 2.4 ± 0.8 PgC year^{-1} and 0.2 PgC year^{-1} in northern and southern mid-latitude lands, respectively, were offset to some degree by a net tropical land source of 1.2 ± 1.2 PgC year^{-1} (Gurney et al. 2002). Adjustment for riverine fluxes (Aumont et al. 2001) yields a net northern terrestrial sink of 2.1 PgC year^{-1} (**Table 3**). In contrast, the flux of carbon from changes in land use in this region is estimated to have been a source of 0.06 PgC year^{-1} during the 1980s, changing to a sink of 0.02 PgC year^{-1} during the 1990s (Houghton 2003). The accumulation of carbon in regrowing forests (following harvest) and in wood products was largely offset by the losses of carbon from decay of wood products and slash (woody debris left on site at harvest). The two approaches suggest a large sink in ecosystems unaffected by land-use change.

That sink is not observed in forests. Forest inventories in northern mid-latitudinal lands systematically measure wood volumes from more than a million plots throughout the region. They provide an independent estimate of change in carbon storage. One recent synthesis of these forest inventories found a net sink of between 0.6 and 0.7 PgC year^{-1} for the years around 1990 (Goodale et al. 2002). The estimate is approximately 30% of the sink inferred from atmospheric data (**Table 3**).

Some of the difference may be explained if non-forest ecosystems in these regions are also accumulating carbon. Inventories of carbon stocks in non-forest lands are generally lacking, but analyses in the United States suggested that non-forests might account for 40%–70% of the net terrestrial carbon sink (Houghton et al. 1999, Pacala et al. 2001). Much of the sink in non-forests was attributed to woody encroachment, the invasion and spread of woody shrubs into formerly herbaceous lands, especially in the southwestern United States. Recent studies have called these estimates into question. Increases in aboveground carbon stocks through woody encroachment can be offset by losses in belowground carbon stocks, leading to a net loss rather than accumulation of carbon (Jackson et al. 2002). Furthermore, in large areas of the southwestern United States, the invasion of non-native annual grasses is increasing the frequency and extent of fires and replacing woody shrublands with grasslands (Bradley et al. 2006). The accumulation of carbon in non-forests may be less than previously thought.

It is also possible that forest inventory data underestimates the accumulation of carbon in forest soils. Soil carbon is not directly measured in forest inventories, but estimated with models. However, the few studies that have measured the accumulation of carbon in forest soils have consistently found soils to account for only a small

fraction (<15%) of net carbon uptake by an ecosystem (Richter et al. 1999, Gaudinski et al. 2000, Barford et al. 2001, Schlesinger & Lichter 2001, Bellamy et al. 2005). Thus, despite the fact that the world's soils hold two to three times more carbon than biomass, there is no evidence yet that they account for much of the enhanced terrestrial sink over the past century.

Finally, the discrepancy between estimates obtained from forest inventories and inverse calculations may be explained by differences in the dates of measurements. Top-down measurements based on atmospheric data are sensitive to large year-to-year variations in terrestrial photosynthesis and respiration. Furthermore, model transport errors are largest in northern latitudes (Baker et al. 2006).

The small carbon sink attributable to changes in land use (nearly zero) could indicate analyses of land-use change are incomplete in their accounting of carbon uptake. Alternatively, there may be other mechanisms besides land-use change responsible for the terrestrial carbon sink inferred from differences between forest inventories and inverse methods. However, both the land-use change and the forest inventories give similar estimates for the sink in northern trees (differences generally less than 0.1 PgC $year^{-1}$ in any region) (Houghton 2003), suggesting that forests recovering from past changes in land use (abandoned farmlands, logging, fire suppression) explain the growth measured in forest inventories. The differences between the estimates must be attributed to uncertainties in the estimates of change for non-tree components (woody debris, soils, or wood products).

In sum, top-down methods (atmospheric data and transport models) show a larger terrestrial sink in northern lands than bottom-up approaches (forest inventories or land-use change). Non-forest systems are implicated, but the evidence is weak. The relative importance of different mechanisms remains unclear.

4.3.2. The tropics. How do different methods compare in the tropics? Inverse calculations with atmospheric data show that tropical lands were a net source of carbon, 1.2 ± 1.2 PgC $year^{-1}$ for the period 1992–1996 (Gurney et al. 2002). The errors in this approach are larger for the tropics than the non-tropics because of the lack of CO_2 sampling stations and the more complex atmospheric circulation there. Accounting for the effects of rivers (Aumont et al. 2001) suggests a net terrestrial source of 1.5 ($\pm$1.2) PgC $year^{-1}$ (**Table 3**).

Changes in land use in the tropics are clearly a source of carbon to the atmosphere, although the magnitude (0.5 to 3.0 PgC $year^{-1}$) is uncertain, in part because estimates of deforestation are uncertain (Fearnside 2000, DeFries et al. 2002, Houghton 2003, Achard et al. 2004) and in part because estimates of biomass are uncertain (Houghton et al. 2001, Eva et al. 2003, Fearnside & Laurance 2003, Houghton 2005).

Forest inventories for large areas of the tropics are rare and, thus, cannot be used to infer sources or sinks. However, repeated measurements of biomass on permanent plots throughout the tropics suggest that undisturbed tropical forests in South America may be accumulating ~0.6 ($\pm$0.3) PgC $year^{-1}$ (Phillips et al. 1998, Baker et al. 2004, Malhi & Phillips 2004). Direct measurement of CO_2 fluxes over unmanaged forests in the Brazilian Amazon (a fourth approach) shows these sites to be both sources (Saleska et al. 2003) and sinks (Grace et al. 1995).

The results from these different approaches (**Table 3**) suggest at least two, mutually exclusive interpretations for the net terrestrial source of carbon from the tropics. One interpretation is that a large release of carbon from land-use change (Fearnside 2000, Houghton 2003) is partially offset by a large sink in undisturbed forests (Phillips et al. 1998, Baker et al. 2004, Malhi & Phillips 2004). The other interpretation is that a modest source of carbon from deforestation (DeFries et al. 2002, Achard et al. 2004) explains the net source, and that the sink in undisturbed forests is nearly zero (Saleska et al. 2003, Rice et al. 2004). Under the first interpretation, some sort of growth enhancement is required to explain the large current sink in undisturbed forests. Under the second, essentially all of the net flux is explained by changes in land use, and a growth enhancement is not required. A recent inverse calculation using a large data base of oceanic pCO_2 as well as atmospheric measurements, found a higher tropical source from land (1.8 ± 1.1 PgC year^{-1}) (Jacobson et al. 2005). This result strengthens the argument that there is not a large carbon sink in the tropics offsetting the source from deforestation.

Distinguishing between recovery (regrowth) and enhanced growth is important, whether in or out of the tropics. If regrowth is dominant, the current sink may be expected to diminish as forests age (Hurtt et al. 2002). If enhanced growth is important, the magnitude of the carbon sink may be expected to increase, at least in the near future. The carbon models used to calculate future concentrations of atmospheric CO_2 have assumed the latter (that the current terrestrial sink will increase), in part because enhanced growth is the mechanism assumed to explain the current terrestrial sink. But if analyses of land-use change have underestimated recovery processes, the assumption of enhanced growth may be invalid, and future projections of climate based on this assumption may underestimate the extent and rate of climatic change.

5. FUTURE CHANGES IN THE CARBON CYCLE: DIMINISHED SINKS AND INCREASED SOURCES OF CARBON?

Both oceanic and terrestrial sinks have increased over the past ~150 years (**Figure 4**). Before 1930, terrestrial ecosystems were nearly neutral (**Figure 3**), but since then the fractions of total emissions accumulating in oceanic, terrestrial, and atmospheric reservoirs, although variable year-by-year, seem not to have changed systematically over time (**Figure 5**). The carbon cycle was behaving in 2000 as it was in 1958. Will the system remain stable? Will the fraction of total emissions (fossil and land-use change) that remains in the atmosphere continue to average 40%–50%?

5.1. Recent Developments

5.1.1. Observations. A few recent observations suggest that the airborne fraction of anthropogenic CO_2 may be increasing. First, there is the observation that the northern hemisphere carbon sink has diminished since 1992 (Miller et al. 2005). The evidence is based on the observation that the north-south difference in CO_2 concentrations is 1 ppm larger in 2003 than it was in 1992. The difference cannot be explained by the increased emissions from fossil fuels (Miller et al. 2005). Furthermore, the

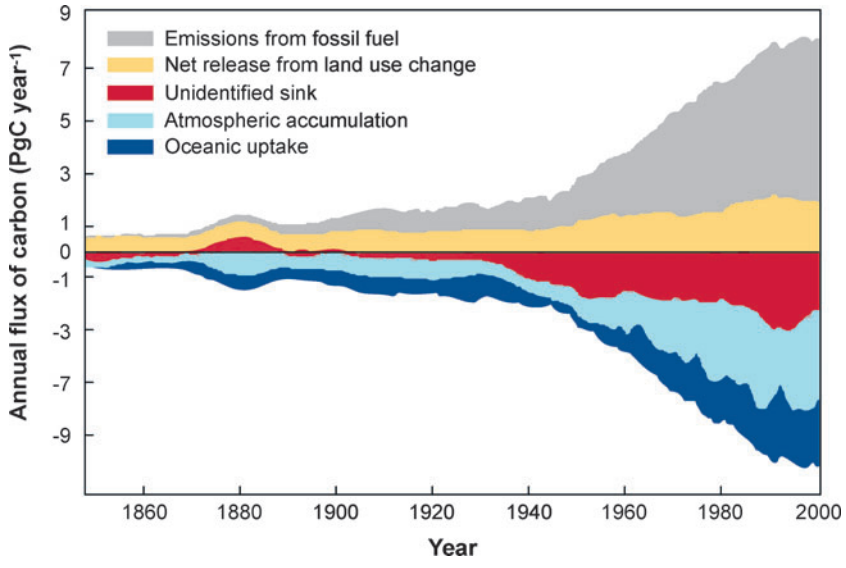

Figure 4

Annual sources and sinks of carbon from 1850 to 2000 for a balanced carbon budget (total sources are balanced by total sinks). The unidentified sink is the residual terrestrial sink.

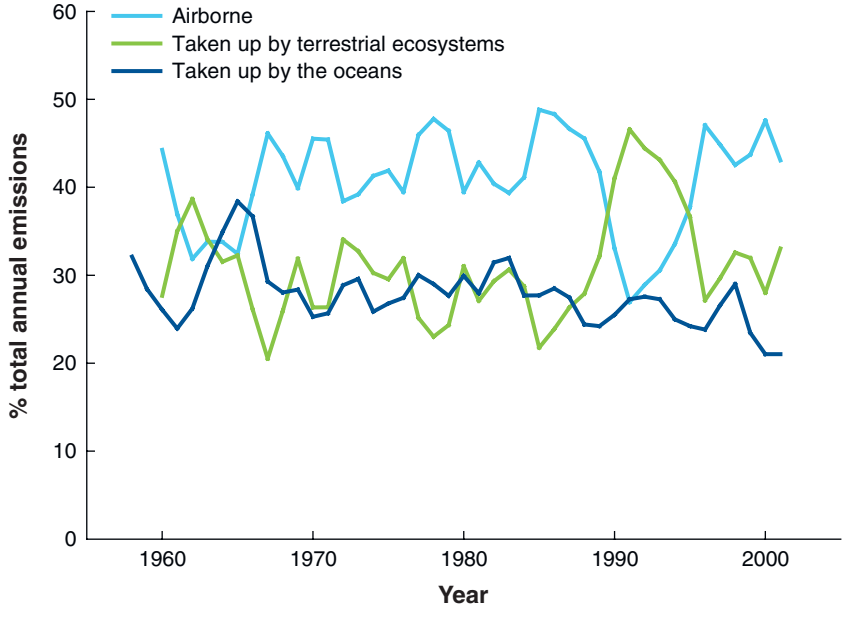

Figure 5

The fractions of total annual emissions (fossil fuel plus land-use change) accumulating in the atmosphere, oceans, and land (from Canadell et al. 2007). The anomaly in the early 1990s coincides with the eruption of Mt. Pinatubo in 1990. The values are 5-year running averages.

uptake of carbon by the oceans seems to have increased (Keeling et al. 2005), suggesting that the diminished sink is terrestrial. Other, longer-term evidence suggests that the efficiency of oceanic uptake may also have declined. pCO_2 in the North Atlantic, a major sink region, indicates a reduced uptake of CO_2 over the past 20 years (Lefèvre et al. 2004). Furthermore, the oceanic uptake of CO_2 emissions decreased from ~44% during the period 1800–1979 to ~36% over the period 1980–1999 (Sabine et al. 2004). The difference was not statistically significant, but it represents the expected trend (Section 3.1.3).

A recent decline in the terrestrial carbon sink is clearer. From measurement of the atmospheric O_2/N_2 ratio and CO_2 concentrations, the net terrestrial uptake is estimated to have declined from 1.2 ± 0.8 PgC year^{-1} over the period 1990–2000 to 0.5 ± 0.7 PgC year^{-1} over the period 1993–2003 (Keeling et al. 2005). Preliminary results suggest that the anomalous growth rates of atmospheric CO_2 concentrations in 2002 and 2003 were both attributable to anomalously high releases of CO_2 from land (Allison et al. 2005). The anomalous emissions were from the tropics in 2002 and from Eurasia in 2003. The 2003 summer heat wave and drought in Europe is estimated to have reduced primary productivity there by 30%, resulting in an anomalous net source of 0.5 PgC (Ciais et al. 2005). Furthermore, both years had large fires, particularly in Siberia (Simmonds et al. 2005), and both years included drought-induced die-off of overstory trees in the southwestern United States (Breshears et al. 2005). The years 2002 and 2003 are the first consecutive years to show a greater than 2 ppm year^{-1} increase in atmospheric CO_2 at Mauna Loa. If climate change is weakening the natural carbon sink, the rate of increase may be expected to accelerate (Jones et al. 2005).

Two years do not establish a trend, of course, but 2005 was another year that showed a greater than 2 ppm rise in atmospheric CO_2. These recent observations, together with the observation that most of the year-to-year variability in the growth rate of CO_2 concentrations results from terrestrial fluxes (Patra et al. 2005, Baker et al. 2006), underscore the tenuous nature of the terrestrial carbon sink (Miller et al. 2005). The following section addresses whether the current carbon sink may be expected to continue.

5.1.2. Results from coupled carbon-climate models. A number of coupled carbon-climate models have been developed to evaluate the potential effects of feedbacks in amplifying or retarding the warming expected from increased concentrations of CO_2 in the atmosphere (Cox et al. 2000; Friedlingstein et al. 2001, 2006). The results are variable (Friedlingstein et al. 2003, 2006) but generally show a net positive feedback or an amplification of the warming predicted to result from anthropogenic addition of greenhouse gases to the atmosphere. The findings are in sharp contrast to the previous generation of climate projections, which were based on the assumption that the current terrestrial sink would grow.

5.1.3. Results from analysis of the paleo record. The effect of CO_2 (and other greenhouse gases) on Earth's temperature is reasonably well constrained. The change in global mean surface temperature for a doubling of CO_2 (temperature sensitivity)

is calculated to range between 1.5 and 4.5°C. The effect of temperature on the CO_2 concentration (feedback) is not well constrained. Two recent studies have used the changes in temperature and CO_2 concentration recorded in ice cores to calculate this feedback. Using data over the period 1200 CE to 1700 CE (including the Little Ice Age), Scheffer et al. (2006) factored out temperature changes directly attributable to the greenhouse effect and determined that carbon feedbacks to climate amplified the warming by 1.15 to 1.78°C, depending on the temperature data used for the reconstruction. A similar analysis based on CO_2 and CH_4 data from the Vostoc ice core (the past 360,000 years) found that the feedback would raise estimates of warming for a doubled CO_2 concentration by as much as 1.5°C (Torn & Harte 2006). Both studies found that global warming should lead to additional sources of carbon.

5.2. Managing the Carbon Cycle

The UNFCCC and Kyoto Protocol are based on the assumption that the nations of the world can manage the global carbon cycle by reducing current emissions of carbon from fossil fuels and by enhancing sinks of carbon. On the order of 100 PgC might be sequestered on land by 2050 through management of forests and agricultural soils. The amount of carbon potentially sequestered is small relative to projected emissions of CO_2 from business-as-usual energy practices, and thus the terrestrial options for sequestering carbon are best viewed as temporary, buying time for the development and implementation of longer-lasting measures for reducing fossil fuel emissions (Watson et al. 2000). Schemes for increasing the storage of carbon in the oceans include stimulation of primary production with iron fertilization (Falkowski et al. 1998, Martin 1990) and direct injection of CO_2 at depth (Herzog et al. 2000). Capture of CO_2 and sequestration in geological formations are also being evaluated (Herzog et al. 2000), as are other mineralogical techniques (Lackner 2003). The technical and economic aspects of an operational sequestration program require considerable research.

Managing carbon would become a much greater challenge if, in addition to managing fossil fuel emissions, society had to deal with new sources (or reduced sinks) of carbon from land and sea. Yet higher temperatures might reduce the current oceanic and terrestrial sinks, leading to higher concentrations of CO_2 than predicted (Woodwell 1983, Woodwell & Mackenzie 1995). Future sources of carbon as a result of positive feedbacks to the warming might be large enough to render carbon management inconsequential. The following section reviews the feedbacks that influence oceanic and terrestrial carbon pools.

5.3. Oceanic Feedbacks in the Carbon-Climate System

Increasing the concentration of CO_2 in the atmosphere is expected to affect the rate of carbon uptake by the oceans through a number of mechanisms, most of them physical or chemical, but some of them biological. The best understood of the mechanisms act to reduce carbon uptake.

5.3.1. The buffer factor. An important aspect of the buffer factor is that as the ocean's carbon inventory increases, the ocean becomes more resistant to taking up additional CO_2. The concentration of carbonate ions decrease, and further additions of CO_2 remain as dissolved CO_2 rather than being converted to HCO_3^-. The ocean becomes more acidic and less effective in taking up additional CO_2. The effect is large. The change in DIC for a 100 ppm increase above 280 ppm (preindustrial) was 40% larger than a 100 ppm increase would be today. And the change in DIC for a 100 ppm increase above 750 ppm would be 60% lower than it is today (Prentice et al. 2001). Thus, as concentration of CO_2 in the atmosphere increases, the fraction of annual emissions going into the ocean decreases, increasing the fraction that is airborne (a positive feedback).

Increased acidity (reduced supersaturation of $CaCO_3$ minerals) of surface waters (in response to the oceanic uptake of CO_2) has been measured (Feely et al. 2004) and suggests that calcification by reef-building corals and some planktonic mussels has declined as a result. However, the precipitation of $CaCO_3$ increases the pCO_2 and acidity of seawater (just as the dissolution of $CaCO_3$ neutralizes acid) (Takahashi 2004), so a reduction in calcification, although harmful for marine organisms, allows the ocean to take up more CO_2. The reduced calcification is a negative feedback to climate warming.

5.3.2. Direct effects of temperature. The fact that the solubility of CO_2 in seawater decreases with temperature represents a direct positive feedback to global warming. A 1°C warming of the ocean temperature increases the equilibrium pCO_2 in seawater (and thus the concentration in the atmosphere) by 10–20 ppm.

5.3.3. Indirect effects of temperature. The ocean's solubility pump is driven by vertical mixing and variations in temperature as well as on the carbon chemistry of seawater. The solubility pump results from the fact that CO_2 is approximately two times more soluble in the cold surface waters of Arctic and Antarctic regions than it is in the warm surface waters near the equator. Because mid-depth and deep waters are formed by the sinking of these cold (high CO_2) surface waters, the CO_2 concentration of the atmosphere is lower than would be in equilibrium with the average concentration of surface waters. Any process that lowers the density of these high-latitude surface waters (for example, melting ice, increased precipitation, or increased river discharge) may reduce the solubility pump. In one model simulation, modest rates of warming reduced the rate of oceanic uptake of carbon, but the reduced uptake was largely compensated by changes in the marine biological cycle (Joos et al. 1999a). For higher rates of global warming, however, the North Atlantic Deep Water formation collapsed and the concentration of CO_2 in the atmosphere was 22% (and global temperature 0.6°C) higher than expected in the absence of this feedback.

The warming of surface waters decreases their density. Because the warming of the oceans will take place in the surface layers first, the warming may increase the stability of the water column. Greater stability of the water column, in turn, will reduce mixing between surface and deeper waters, slowing oceanic uptake further (a positive feedback). Similarly, if the warming of Earth's surface is greater at the poles than at

the equator, the latitudinal gradient in surface ocean temperature will be reduced; and because that thermal gradient plays a role in the intensity of atmospheric mixing, a smaller gradient might be expected to subdue oceanic mixing and increase stagnation. As the most important process in slowing the oceanic uptake of CO_2 is the rate of vertical mixing between the surface and the deep ocean, a reduction in the intensity of circulation may be expected to slow the rate of oceanic carbon uptake.

5.3.4. Biological processes. Marine productivity is often limited by nutrients, in particular nitrogen (N). As most of the N for marine production comes from upwelling, physical changes in ocean circulation will affect primary production and, hence, the biological pump. However, although increased temperature increased vertical stratification in six different ocean models, the net effect of the changes in temperature and stratification was to increase primary productivity between 0.7% to 8.1% (Sarmiento et al. 2004). The variation resulted largely from uncertainty in the temperature sensitivity of primary production.

Some N is also made available through N fixation, and some is lost through denitrification, both of which are biological processes limited by trace nutrients and the concentration of oxygen. Differential changes in either one would affect the inventory of fixed N in the ocean and, thereby, productivity and the biological pump. How these processes might be affected by changes in climate or vertical mixing is unclear.

Large regions of the ocean are not limited by N or P (phosphorus), and in these regions primary productivity stops before the available N and P have been used up. It has been hypothesized that the limiting nutrient is iron, and that additions of iron would enhance the utilization of N and P, thereby increasing productivity (Martin 1990). Iron might become more available indirectly as a result of increased human eutrophication of coastal waters. Or, as the aeolian transport of iron in dust is a major source of iron for the open ocean, iron could either increase or decrease in the future, depending on changes in the distribution of precipitation on land (Falkowski et al. 1998).

Finally, productivity might increase if the Redfield ratio (C:N:P) of phytoplankton were to widen; that is, if more carbon could be sequestered for the same amount of N or P. The effect on productivity would be the same as adding N. The recent observation that the C:N:P ratio of dissolved organic carbon (DOC) is much greater than it is for particulate organic carbon (POC) suggests that DOC is a more efficient exporter of carbon to the deep ocean (Hopkinson & Vallino 2005). Processes that would increase the production of DOC relative to POC, as well as processes that widen the C:N:P ratio, could lead to a higher productivity and a greater uptake of carbon.

All of these biological factors that could enhance the biological pump are largely possibilities, however. Their role in changing the distribution of carbon between atmosphere and ocean is less certain than the role that chemical and physical feedbacks play in controlling oceanic uptake of anthropogenic carbon.

5.3.5. Rate of CO_2 emissions. High rates of CO_2 emissions will increase the atmosphere-ocean gradient in CO_2 concentrations and thus increase the rate of carbon uptake by surface waters. However, the increased gradient will not change

the rate at which surface waters are mixed with the deeper layers (the bottleneck in oceanic uptake). Thus, the higher the rate of CO_2 emissions, the greater the airborne fraction. This process is not strictly a feedback, but it does affect the rate at which CO_2 increases in the atmosphere. Under the business-as-usual scenario for future CO_2 emissions, rates of emissions increase by nearly a factor of 3, from approximately 7 PgC year^{-1} today to ~20 PgC year^{-1} by the end of the twenty-first century.

5.4. Terrestrial Feedbacks in the Carbon-Climate System

The need for a terrestrial sink to balance the global carbon budget has focused attention on identifying and evaluating possible mechanisms for such a sink. In contrast, relatively little research has been concerned with the possibility of additional terrestrial sources of carbon. As a result of recent evidence that Earth's climate is changing, the balance of research has begun to shift. The concern is that the present terrestrial carbon sink may not persist (Canadell et al. 2007a).

5.4.1. CO_2 fertilization. Despite the initial increases in productivity and biomass observed in crops, annual plants, and tree seedlings under elevated concentrations of CO_2, experiments at the level of ecosystems and experiments longer than a few years suggest much reduced responses. Plants often acclimate to higher concentrations of CO_2 so that their rates of photosynthesis and growth return to the rates observed at ambient levels (Oren et al. 2001, Tissue & Oechel 1987, Waterhouse et al. 2004). Furthermore, productivity is not equivalent to carbon storage. If an increase in productivity is in tissues with a rapid turnover (fine roots, foliage), the enhanced growth may be respired within a year or two, leading to little or no gain in carbon storage (Davidson & Hirsch 2001, Schlesinger & Lichter 2001).

CO_2 fertilization experiments longer than a few years in whole ecosystems often show an initial CO_2-induced increment in biomass that diminishes over time. The diminution of the initial response occurred after two years in an arctic tundra (Oechel et al. 1994) and after three years in a rapidly growing loblolly pine forest (Oren et al. 2001). The pine forest was chosen in part because CO_2 fertilization was expected to be greatest in a rapidly growing forest. The decline in the initial stimulation is thought to occur because some factor other than CO_2 becomes limiting. As N is often a limiting nutrient in temperate zone ecosystems, several studies have investigated the interaction between C and N. The results are mixed. In two forests, enhanced productivity continued for six years, in part, because the C/N ratio in the high CO_2 treatment increased, and in part because the elevated CO_2 stimulated root growth and tapped a larger volume of soil for N (Finzi et al. 2006, Norby & Iversen 2006). In another forest (Hungate et al. 2006) and in two grasslands (Gill et al. 2006, Reich et al. 2006), productivity declined, although changes in the allocation of N between plants and soil served to delay the nutrient-induced decline. Because the results of these experiments are consistent with the accumulation of C and N during succession over hundreds to millions of years, the investigators hypothesize that ecosystems may have some intrinsic capability to stimulate N accumulation through carbon input (Luo et al. 2006).

The hypothesis is particularly relevant to model predictions of large terrestrial carbon sinks during the twenty-first century (Cramer et al. 2001). Those models predicting large carbon sinks did not include N in their simulations, and it is unclear that the N, as well as other nutrients necessary for this cumulative sink, will be available (Hungate et al. 2003). Even if CO_2 fertilization is an important mechanism explaining the current carbon sink on land, its persistence in the future is uncertain.

5.4.2. Nitrogen, sulfur, and ozone. Adding N to forests often increases productivity (Bergh et al. 1999, Magill et al. 2000), and it may also modify soil organic matter so as to increase its residence time (Bryant et al. 1998, Fog 1988). But N deposited in ecosystems may also be immobilized in soils (Nadelhoffer et al. 1999) or lost from the ecosystem, becoming largely unavailable in either case (Davidson 1995). Furthermore, although additions of N may increase the storage of carbon in plants, they may decrease its storage in soil and in the whole ecosystem (Mack et al. 2004). High levels of N may also saturate ecosystems, eventually reducing productivity (Makipaa 1995, Tamm et al. 1995, Aber et al. 1998, Fenn et al. 1998). The long-term effects of N deposition on forest production and carbon balance remain uncertain.

The story is complicated because much of the nitrogen deposited on land is in the form of acid precipitation, and it is difficult to distinguish the fertilization effects of nitrogen from the adverse effects of acidity. Other factors, such as tropospheric ozone and sulfur (acid rain), also reduce productivity, but the magnitude of the global effect is unknown. The pollutants could potentially increase carbon stocks if they reduced decomposition of organic matter more than they reduced productivity. Interestingly, regions where N inputs are high are often regions where ozone concentrations are also high, and the effects may be largely offsetting in terms of productivity (Ollinger et al. 2002).

5.4.3. Climatic variability and climatic change. Year-to-year differences in the growth rate of CO_2 in the atmosphere are large (**Figure 2**) and are attributed for the most part to variations in terrestrial metabolism (and fires) caused by variations in climate (Patra et al. 2005, Baker et al. 2006). Measurements at individual ecosystems (Valentini et al. 2000, Saleska et al. 2003) and at continental and global scales (Myneni et al. 1995, Behrenfeld et al. 2001, Hicke et al. 2002) suggest that respiration is more sensitive than photosynthesis to variations in climate (see Chen et al. 2006 for an exception).

Short-term variations in atmospheric CO_2 may not be adequate for predicting longer-term trends, however. Organisms and populations acclimate and adapt, if possible, diminishing short-term responses, whether to CO_2 (Tissue & Oechel 1987) or to temperature (Luo et al. 2001). At the other extreme, long-term or equilibrium effects of climate on carbon storage indicate that cool, wet habitats store more carbon in soils than hot, dry habitats (Post et al. 1982, Wynn et al. 2006). The transient effects of climatic change over intermediate timescales are the more difficult changes to predict. Over decades to centuries the factors most important in influencing concentrations of atmospheric CO_2 (fossil fuel emissions, land-use change, oceanic

uptake) are probably different from the factors important in year-to-year variations in atmospheric CO_2.

Despite a number of recent experiments and analyses, there is no consensus as to the temperature sensitivity of upland mineral soils to decomposition (respiration) (Davidson & Janssens 2006, Kirschbaum 2006). The few multi-decade surveys over large areas have not yielded consistent results. Changes in soil organic matter observed over a 25-year period across England and Wales indicated a net loss of carbon at a mean rate of 0.6% $year^{-1}$ from all types of soil (Bellamy et al. 2005). The fact that the losses occurred independent of land use suggested that climate was the driving factor. In contrast, half of the 289 landscape units examined in Belgium showed an increase in soil organic carbon between 1960 and 2000 (Lettens et al. 2005). The uncertain temperature sensitivity of organic carbon in upland mineral soils does not apply to all soils, however (Davidson & Janssens 2006). The factors limiting decomposition in wetlands, peatlands, and permafrost soils are reasonably well understood. Not only do these ecosystems hold a substantial amount of terrestrial carbon, they are also likely to be affected by changes in climate (Davidson & Janssens 2006).

Arctic and boreal lands, in particular, are of considerable interest because of their large reserves of soil carbon and the greater warming anticipated for high latitudes. Satellite observations of these regions initially indicated an increase in the greenness of boreal and temperate forests (Myneni et al. 1997), interpreted as an increase in productivity. The warming was perhaps increasing the terrestrial carbon sink. More recent analyses confirm the increased greening of tundra, but show a trend of reduced productivity in some of the forests after ~1990 (Angert et al. 2005, Goetz et al. 2005, Bunn & Goetz 2006), perhaps because higher temperatures have contributed to summer droughts (Barber et al. 2000, Lloyd & Fastie 2002). Measurements of CO_2 flux in these ecosystems show variable responses to warm temperatures (Oechel et al. 1993, Goulden et al. 1998, Heikkinen et al. 2004). The issue comes down to whether increased temperatures tip the balance toward greater photosynthesis and growth (carbon sink) (Chen et al. 2006) or to greater respiration (source). Soil moisture may be even more important than temperature. Furthermore, the effect of temperature (and drought) is confounded with fires, both in boreal regions (Kasischke & Turetsky 2006) and in the tropics (Nepstad et al. 1999, Page et al. 2002).

6. CONCLUSIONS

The current terrestrial carbon sink represents a subsidy that has kept the airborne fraction of total CO_2 emissions between 40% and 50% for at least the past five decades. It would clearly help in management of the carbon cycle if that fraction were to continue or get smaller in the future. If a significant part of the current terrestrial sink is the result of regrowth (changes in age structure), however, the future terrestrial sink is unlikely to resemble the past. First, the sink in (re)growing forests declines as forests age (Hurtt et al. 2002). Second, the net effect of continued land-use change is likely to release carbon, rather than store it. And third, forests that might have accumulated carbon in the past (whatever the cause) are unlikely to function as sinks if they are converted to agricultural lands.

Despite evidence that changes in land use are important in explaining the current terrestrial carbon sink, and despite the expectations that this sink will diminish in the future, most projections of future climate have been based on the assumption that the current terrestrial sink will not only continue but will grow in proportion to concentrations of CO_2. The disparate future predictions among terrestrial carbon models, however, despite their agreement that CO_2 fertilization is responsible for the present sink, suggests that they are not yet reliable enough to determine the mechanisms responsible for the current modest terrestrial sink (Cramer et al. 2001) [a situation shared with ocean carbon models (Matsumoto et al. 2004)]. Even if the physiological mechanisms in terrestrial models were correct, stochastic processes, such as fires, storms, insects, and disease (i.e., disturbance and recovery), have been largely ignored.

There is another reason why the recent sinks on land and in the ocean may decline in the future: the positive feedbacks of temperature on respiration and of increased CO_2 on oceanic uptake. With a few notable exceptions (Kellogg 1983, Lashof 1989, Woodwell & Mackenzie 1995, Lashof et al. 1997), little attention has been given, until recently, to the possibility that global warming may change the balance of terrestrial sources and sinks. The lack of attention to additional sources of carbon can probably be attributed to the preoccupation of the community with finding terrestrial sinks (the so-called missing carbon). In addition, over the past ~150 years both oceanic and terrestrial sinks have generally increased (**Figure 4**). The stability of this trend is remarkable, given the rise of nearly 0.5°C in average surface temperature of Earth in the past three decades, and a warming 3–4 times greater than that average at high latitudes over land (Houghton et al. 2001). The warming has been enough to melt glaciers and sea ice and thaw permafrost but seems not to have changed the fraction of emissions accumulating in the atmosphere, land, and oceans. Are the expected positive feedbacks offset by negative feedbacks, is the system more stable than anticipated, are there lags in the system, or is the net terrestrial sink just now showing the first signs of decline? And will we still be able to manage the carbon cycle by the time we have the answers?

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