

COMMENTARY

# Carbon Metabolism of the Terrestrial Biosphere: A Multitechnique Approach for Improved Understanding

J. G. Canadell,<sup>1\*</sup> H. A. Mooney,<sup>2</sup> D. D. Baldocchi,<sup>3</sup> J. A. Berry,<sup>4</sup>  
J. R. Ehleringer,<sup>5</sup> C. B. Field,<sup>4</sup> S. T. Gower,<sup>6</sup> D. Y. Hollinger,<sup>7</sup> J. E. Hunt,<sup>8</sup>  
R. B. Jackson,<sup>9</sup> S. W. Running,<sup>10</sup> G. R. Shaver,<sup>11</sup> W. Steffen,<sup>12</sup>  
S. E. Trumbore,<sup>13</sup> R. Valentini,<sup>14</sup> and B. Y. Bond<sup>15</sup>

<sup>1</sup>Global Change and Terrestrial Ecosystems (GCTE) International Project Office, Commonwealth Scientific and Industrial Research Organization—Wildlife and Ecology, P.O. Box 284, Canberra, ACT, 2601, Australia; <sup>2</sup>Department of Biological Sciences, Stanford University, Stanford, California 94305, USA; <sup>3</sup>Ecosystem Science Division, Department of Environmental Science, Policy and Management, 345 Hilgard Hall, University of California, Berkeley, Berkeley, California 94720, USA; <sup>4</sup>Department of Plant Biology, Carnegie Institution of Washington, 290 Panama Street, Stanford, California 94305, USA; <sup>5</sup>Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA; <sup>6</sup>Forest Ecosystem Ecology Program, Department of Forestry, University of Wisconsin–Madison, Madison, Wisconsin 53706, USA; <sup>7</sup>USDA Forest Service, Corner of Concord and Mast Roads, Durham, New Hampshire 03824, USA; <sup>8</sup>Landcare Research, P.O. Box 69, Lincoln, New Zealand; <sup>9</sup>Department of Botany, Phytotron Building, Duke University, Durham, North Carolina 27708, USA; <sup>10</sup>School of Forestry, University of Montana, Missoula, Montana 59812, USA; <sup>11</sup>Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543, USA; <sup>12</sup>IGBP Secretariat, Royal Swedish Academy of Sciences, Box 50005, S-10405 Stockholm, Sweden; <sup>13</sup>Earth System Science, University of California, Irvine, California 92717, USA; <sup>14</sup>Department of Forest Science and Environment, University of Tuscia, Via S. Camillo de Lellis, I-01100 Viterbo, Italy; <sup>15</sup>Department of Forest Science, Oregon State University, Corvallis, Oregon 97331, USA

## ABSTRACT

Understanding terrestrial carbon metabolism is critical because terrestrial ecosystems play a major role in the global carbon cycle. Furthermore, humans have severely disrupted the carbon cycle in ways that will alter the climate system and directly affect terrestrial metabolism. Changes in terrestrial metabolism may well be as important an indicator of global change as the changing temperature signal. Improving our understanding of the carbon cycle at various spatial and temporal scales will require the integration of multiple, complementary and independent methods that are used by different research communities. Tools such as air sampling networks, inverse numerical methods, and satellite data (top-down approaches) allow us to study the strength and location of the global- and continental-scale carbon sources and sinks.

Bottom-up studies provide estimates of carbon fluxes at finer spatial scales and examine the mechanisms that control fluxes at the ecosystem, landscape, and regional scales. Bottom-up approaches include comparative and process studies (for example, ecosystem manipulative experiments) that provide the necessary mechanistic information to develop and validate terrestrial biospheric models. An iteration and reiteration of top-down and bottom-up approaches will be necessary to help constrain measurements at various scales. We propose a major international effort to coordinate and lead research programs of global scope of the carbon cycle.

**Key words:** biosphere metabolism; carbon cycle; carbon fluxes; global change; terrestrial ecosystems.

## INTRODUCTION

The world's terrestrial ecosystems are a very large net sink for carbon (C), some years in the range of 3–4 Pg of C and other years in the range of 1–2 Pg (Ciais and others 1995; Schimel and others 1996). This persistent storage occurs in the context of even larger fluxes, with annual gross photosynthesis by land plants and respiration by terrestrial heterotrophs in the range of 100–120 Pg, or approximately 15% of the total C in the atmosphere. The biospheric fluxes of C and other quantities are the result of independent action by countless individual organisms. Yet, these individual organisms interact with each other, with the physical environment, and with anthropogenic impacts in ways that often are consistent across broad ranges of biological diversity. This consistency makes it possible to characterize the function of large collections of organisms, ecosystems, or biomes as aggregated entities that can be treated as individual elements in a global scale analysis. Aggregation has clear advantages for tackling large-scale problems, although the behavior of these individual units, ecosystems, landscapes, and biomes, is not well known.

With an increasing need to understand the role of the terrestrial biosphere in global fluxes of C and other quantities, it is critical to develop a clear understanding of the spatial and time scales in which various processes operate. Global-scale observations, from atmospheric CO<sub>2</sub> to satellite observations of the earth's surface, make it clear that there are consistencies in the response of the biosphere to natural cycles like El Niño Southern Oscillation (ENSO) droughts, as well as to anthropogenic forcings such as increased atmospheric CO<sub>2</sub> or nutrient deposition (Holland and others 1997; Mooney and others 1999)

These observations combined with the opportunities created by new data sets and measurement tools, plus ecological and physiological observations at a range of scales, form the foundation for studying the metabolism of the entire biosphere. There is the need, however, to develop a framework to better integrate measurements that are taken at various scales of time and space by many independent research groups. This integration of measurements of terrestrial biosphere metabolism is critically important as we try to understand the contemporary C cycle and the strength of C sources and sinks with their spatial and temporal variation. In addition, integration is required to predict future growth of atmospheric CO<sub>2</sub> and the associated impacts on the climate system. Both, the changes in global metabolism that are occurring and the need

**Table 1.** IPCC Average Annual Budget of CO<sub>2</sub> Perturbations for 1980–89 (Gt Cy<sup>-1</sup>)

CO <sub>2</sub> sources	
(1) Emissions from fossil fuel combustion and cement production	5.5 ± 0.5
(2) Net emissions from changes in tropical land use	1.6 ± 1.0
(3) Total anthropogenic emissions = (1) + (2)	7.1 ± 1.1
Partitioning amongst reservoirs	
(4) Storage in the atmosphere	3.3 ± 0.2
(5) Ocean uptake	2.0 ± 0.8
(6) Uptake by northern hemisphere forest regrowth	0.5 ± 0.5
(7) Other terrestrial sinks = (3) - [(4) + (5) + (6)] (CO <sub>2</sub> fertilization, nitrogen fertilization, climate effects)	1.3 ± 1.5

Source: Schimel and others (1996).

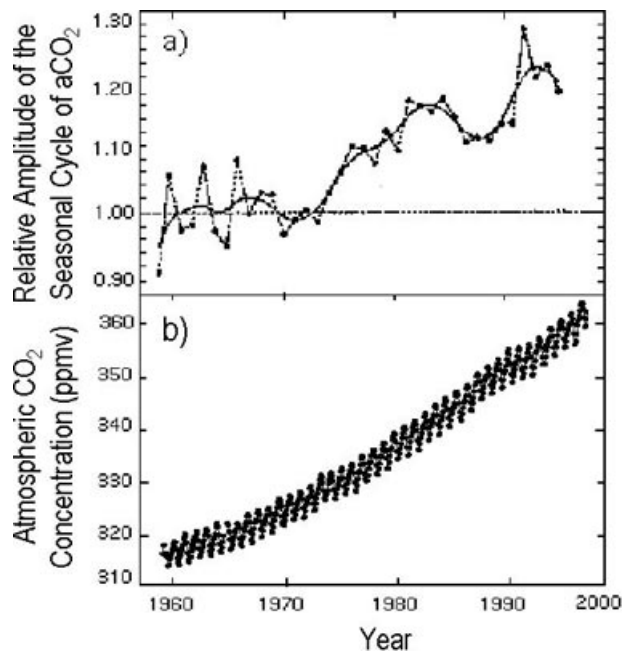
for information to respond to the Framework Convention for Climate Change (FCCC) provide sufficient impetus to initiate an integrated international research effort.

## CURRENT STATUS OF THE TERRESTRIAL CARBON CYCLE

### Overview of the Carbon Cycle

The full C budget for the period of 1980–89 was summarized by the Intergovernmental Panel of Climate Change (IPCC; Schimel and others 1996; Table 1). Average emissions from fossil fuel were 5.5 ± 0.5 Gt C y<sup>-1</sup> (6.1 Gt C y<sup>-1</sup> in 1990), and net emissions due to tropical land-use change were 1.6 ± 1.0 Gt C y<sup>-1</sup>. These C emissions were stored in the atmosphere (3.3 ± 0.2 Gt C y<sup>-1</sup>) and in the oceans (2.0 ± 0.8 Gt C y<sup>-1</sup>) for which measurements are best constrained. These measurements, however, required a large terrestrial sink to balance the global budget, the so-called missing carbon. During the decade of 1980s, this sink was on average 1.8 ± 1.6 Pg C y<sup>-1</sup> and was roughly offset by the estimated C emission from land-use change in the tropical regions.

This terrestrial sink, however, shows spatial and temporal variations as large as 3–4 Pg C y<sup>-1</sup> due most likely to different land-use patterns, vegetation types, and interannual climate variability (for example, ENSO). Independent data show that a significant part of this terrestrial C sink is located in the midlatitudes of the Northern Hemisphere (Tans and others 1990; Ciais and others 1995). However, large



**Figure 1.** Trends in atmospheric CO<sub>2</sub> at Mauna Loa Observatory, Hawaii. (a) Relative amplitude of the seasonal cycle of atmospheric CO<sub>2</sub> (Keeling and others 1996), reprinted with permission from Nature; (b) Atmospheric CO<sub>2</sub> concentrations (ppmv) derived from in situ air samples collected from 1958 to 1996 (Keeling and Whorf 1998).

uncertainties exist as to what processes and forcing factors cause the inferred terrestrial sink. Increasing atmospheric CO<sub>2</sub> and nitrogen (N) fertilization presumably play a role, as does climate variability, afforestation (that is, forest regrowth in previously cultivated lands), and reforestation. Direct measurements to detect the responsible processes and forces are unfortunately lacking. Recent model analyses have suggested that the “missing carbon” could be explained by the CO<sub>2</sub> fertilization effect (Taylor and Lloyd 1992; Thompson and others 1996). The suggestion is that the C sink is the result of the disequilibrium between the increasing primary production (as atmospheric CO<sub>2</sub> increases) and respiration of the carbon pools (litter and soil organic matter) that lags behind by some years to decades; the net balance remains positive as long as the atmospheric CO<sub>2</sub> continues growing.

Analysis of CO<sub>2</sub> data from an air sampling network has identified significant interannual variation in the intensity of CO<sub>2</sub> exchange of the land surface and a secular trend of increasing annual oscillation in CO<sub>2</sub> concentration, particularly at high northern latitudes (Figure 1). ENSO has been undoubtedly associated with the interannual variability of the terrestrial C sink (Bacastow 1976; Keeling and

others 1995). For instance, undisturbed Amazonian ecosystems act as C sources during hot and dry ENSO years and as C sinks during non-ENSO years (Tian and others 1998). Keeling and others (1995) suggested that the increased seasonal exchange of CO<sub>2</sub> is associated with a longer growing season (an advance of approximately 1 week in the onset of the spring drawdown of CO<sub>2</sub>). This latter trend was confirmed by the analysis of a satellite record extending from 1982 to 1990, which showed a significant increase in greenness at high northern latitudes (Myneni and others 1997).

In summary, the terrestrial metabolism is highly dynamic and complex as reflected by seasonal, interannual, and decadal variability, as well as underlying increasing atmospheric CO<sub>2</sub> since the time of the Industrial Revolution (Figure 1). However, our ability to predict future CO<sub>2</sub> dynamics of the terrestrial biosphere is limited because of uncertainties in the rates and effects of land-use change, CO<sub>2</sub> and N fertilization, and climate sensitivity of the C cycle.

#### Available Tools and Data Sets

Understanding the current status of terrestrial C metabolism requires integration of diverse measurements and modeling approaches. A number of tools are important for scaling up C metabolism of ecosystems to larger regions (for example, landscape, continental and global), and to scale down from continental to ecosystem measurements. Below we describe the data sets and tools that are the foundations of our current understanding of the ecosystem and global C cycle.

**Global data sets.** Data sets exist for land-cover classification and for the major components of the C budget, some of which were developed under the International Biological Program (IBP). Land-cover classification schemes range from simple categories based on physiognomy that can be remotely sensed (Nemani and Running 1996) to more detailed classifications that include climate and other variables (Prentice 1990; Melillo and others 1993). A 1-km resolution global land-cover database was derived from Advanced Very High Resolution Radiometer (AVHRR) and is available for use in a wide range of environmental research and modeling applications (Belward 1996).

Data on global soil C content are available and have been used to develop global distribution maps (Post and others 1982). Content of soil C in deep horizons (1–3 m) is available at the biome-level (Jobbagy and Jackson 1999). Global data sets also exist for key processes and components of ecosystem metabolism such as litter production and turnover (Mathews 1997), root distributions (Jackson and others 1996), and maximum rooting depth

(Canadell and others 1996). National forest inventories, most commonly available for boreal and temperate regions, are important data sets for above-ground C stocks and net primary productivity (NPP) at a coarse time scale (greater than 5 years; Houghton 1999; Houghton and Hackler 1999; Kurz and Apps 1999).

The combination of all these data sets form the basis for model parametrization and validation of NPP and net ecosystem productivity (NEP) model results. For instance, there are numerous global estimates of terrestrial NPP derived from models of varying ecological complexity (Cramer and others 1999), although only very sparse multiyear ground-based data sets on NPP measurements currently exist (Scurlock and others 1999).

*Land-use change and biomass burning.* Changes in land use are estimated to have contributed approximately 25% to the enhanced greenhouse effect, calculated on the basis of human-caused emissions of greenhouse gases (Houghton 1990). Fluxes associated with land-use change include burning used to clear ecosystems for agriculture, C emissions from organic matter decay (that is, decomposition), and C uptake by forest growth after harvest and shifting cultivation. Fluxes from land-use change in nine regions of the globe added 124 Pg C to the atmosphere during the period 1850–1990 (Houghton 1999; Regions: North America, Europe, the former Soviet Union, Pacific developed region, China, South and Central America, North Africa–Middle East, tropical Africa, and south and Southeast Asia).

Biomass burning, which includes both wildfires and burning after harvest for land clearing, contributes as much as 40% of the total global pyrogenic carbon emissions (Mack and others 1996). A biomass burning inventory has been initiated by the National Aeronautics and Space Administration/Distributed Active Archive Center that will provide the number of fires and hectares burned worldwide from satellite information (Sproles 1996).

*Remote sensing.* The pioneering research of Tucker and others (1986) showed a strong correlation between a satellite-derived vegetation index [Normalized Difference Vegetation Index (NDVI)] and the photosynthetic drawdown of atmospheric CO<sub>2</sub>. Fung and others (1987) developed a model based on monthly maps of NDVI obtained from the National Oceanic and Atmospheric Administration-Advance High Resolution Radiometer satellite and global temperature data to construct monthly maps of net C exchange between the terrestrial biosphere and the atmosphere. These fluxes were mixed using a tracer model based on the Goddard Institute for Space Studies Global Circulation Model to construct

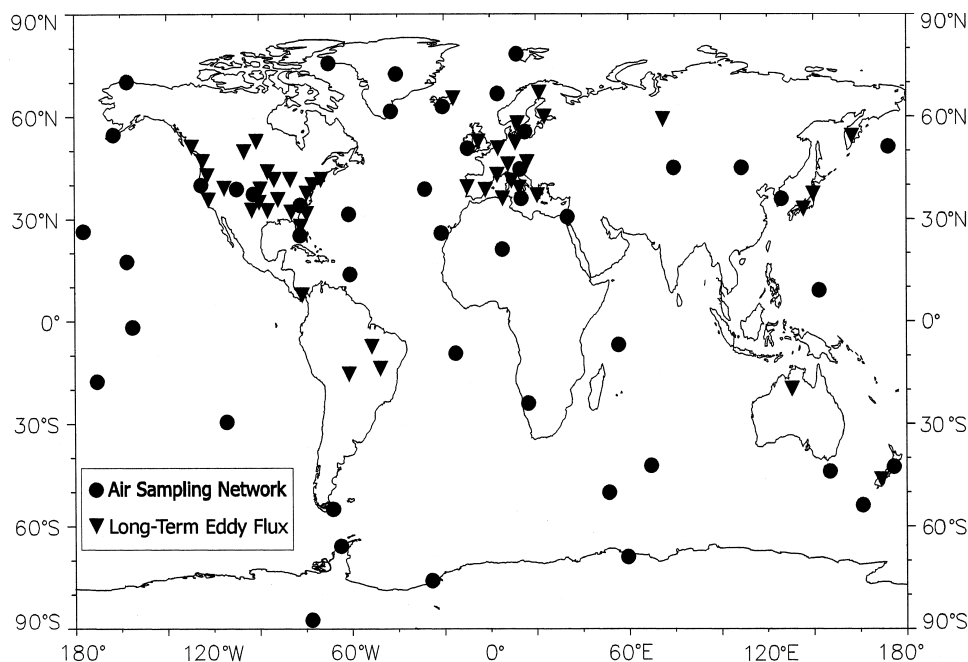
global estimates of atmospheric CO<sub>2</sub> concentrations. The biosphere model, calibrated against NPP measurements, largely with data from IBP, reproduced the seasonal phase and latitudinal pattern of the observed variation in atmospheric CO<sub>2</sub>. More recently, Knorr and Heimann (1995) estimated global NPP deriving leaf area and phenology from NDVI data. We now have a record extending more than a decade of both atmospheric CO<sub>2</sub> and satellite measurements of NDVI, corrected for atmospheric effects and sensor drift.

*Terrestrial biospheric models.* There has been significant progress in the past decade in the sophistication of models used to simulate surface fluxes of CO<sub>2</sub> and its isotopic composition from the terrestrial biosphere (see Heimann and others 1998; Cramer and others 1999). An array of new global models make direct use of satellite data to describe seasonal phenology and the density of vegetation. They use process-based models of photosynthetic and respiratory metabolism to simulate key ecosystem processes. Other models are based on regressions between environmental factors and ecosystem functions (for example, NPP, NEP), and most of them are grid-based so that they can estimate fluxes from global to regional scales. They also can be run online with a global circulation model (GCM) that mixes the CO<sub>2</sub> in the atmosphere, producing interactive simulations of atmospheric CO<sub>2</sub> concentration. The models also can be run with assimilated climates generated by numerical weather forecasting process models to produce estimates of biosphere responses to climate. These coupled models are poised for climate analyses examining the interannual and secular variations in global atmospheric CO<sub>2</sub> concentrations.

Models are the only integrative tool that can simulate future carbon fluxes under global environmental change. For this purpose, only models based on process information have a prognostic value. These are the terrestrial biogeochemistry models (TBMs; for example, Kicklighter and others 1999) and the dynamic global vegetation models (DGVMs; for example, Foley and others 1996). TBMs have a fixed geographic distribution of ecosystem types, and DGVMs take into account climate-induced change in ecosystem structure and composition.

*Global air sampling network (Flask Network).* The relatively slow latitudinal mixing of the atmosphere, and the fact that sources and sinks of CO<sub>2</sub> are neither uniformly distributed over the earth nor uniformly active in time, results in local departures of CO<sub>2</sub> concentration from the mean global value. Networks of stations for sampling the composition of the atmosphere have been established by Scripps





**Figure 2.** Global air sampling sites network (●) (Conway and others 1994; Ciais and others 2000) and long-term eddy covariance sites (FLUXNET) (▼).

Institution of Oceanography (10 sites), the Commonwealth Scientific and Industrial Research Organization (Australia, five sites), and the National Oceanic and Atmospheric Administration/Climate Monitoring and Diagnostic Laboratory (USA, 20 sites; Tans and others 1996; Figure 2). Other sites have been added to form GLOBALVIEW-CO<sub>2</sub> (Ciais and others 2000). Each network analyzes flask samples of air taken at intervals of 1–3 weeks and determines concentrations of CO<sub>2</sub>; most of the sites also analyze for <sup>13</sup>C-CO<sub>2</sub>, <sup>18</sup>O-CO<sub>2</sub>, O<sub>2</sub>, CO-CFCS, and CH<sub>4</sub>. Most of the stations are located far from large land masses to avoid local land influence, although some stations are at the windward edge of land masses. Thus, the network provides an improved picture of seasonal cycles, latitudinal gradients, and interannual variability. This exchange covers both terrestrial and marine ecosystems and includes the effects of fossil fuel use, biomass burning, and land-use conversion. Analyses of these data depend on models of atmospheric transport and knowledge of the physical and biotic variables that control CO<sub>2</sub> exchange globally over time.

**Eddy covariance.** Eddy covariance measures vertical fluxes of energy, CO<sub>2</sub>, and water vapor between terrestrial ecosystems and the atmosphere over flat terrain, providing a measure of NEP (Table 2). Eddy fluxes are to ecosystem physiology what leaf gas fluxes are to plant physiology. The development of continuous eddy flux measurements in recent years, combined with additional measurements and modeling, have generated a new understanding of ecosystem metabolism at the stand level (1 km<sup>2</sup>). Eddy

flux measurements, when combined with physiological process-level studies, provide critical understanding of environmental controls of NEP.

Many national and international programs using eddy covariance have come together into one international network called FLUXNET (Running and others 1999; Figure 2) that currently consists of 70 operating and planned sites. FLUXNET will develop a database of energy, CO<sub>2</sub>, and water vapor fluxes that could lead to the equivalent of the existing network of flask measurements of atmospheric CO<sub>2</sub> (see Global Air Sampling Network). The eddy covariance approach also is used in tall towers (greater than 400 m; Bakwin and others 1995) and aircrafts (Tans and others 1996).

## FUTURE TRENDS OF THE TERRESTRIAL CARBON CYCLE

The present role of terrestrial ecosystems in the global C budget is unlikely to remain constant as the climate changes and as human dominance of the global landscape proliferates (Vitousek and others 1997; Walker and others 1999). On a 5–50-year time scale, it is unlikely that ecosystem responses to annual climatic variation or short-term climate trends will give us a reliable indication of the magnitude and sign of longer-term changes in C fluxes. For example, initial changes in photosynthesis and respiration in response to warming may not be sustainable in the long-term without corresponding changes in other ecosystem processes with longer responses times, such as N mineralization in

**Table 2.** Estimates of Forest NEP via Eddy Covariance

Reference	Forest Type	NEP Estimate (g C m <sup>-2</sup> y <sup>-1</sup> )	Duration (Months)
Grace and others 1995	Tropical Rain Forest, Brazil	-100	1.5
Greco and Baldocchi 1996	Oak-hickory, Tennessee, USA <sup>a</sup>	-525	12
Valentini and others 1996	Beech, Collelong, Italy <sup>b</sup>	-470	12
M. Goulden and others 1996b	Mixed Deciduous, Harvard Forest, USA <sup>a</sup>	-210	36
N. Jensen and others, unpublished	Beech, Soroe, Denmark <sup>b</sup>	-193	12
M. Aubinet and others, unpublished	Mixed Forest, Vielsalm, Belgium <sup>b</sup>	-400	12
A. Dolman and others, unpublished	Scots Pine, Loobos, Netherlands <sup>b</sup>	-300	12
T. Vesala and others, unpublished	Scots Pine, Hyytiala, Finland <sup>b</sup>	-300	12
Jarvis and others 1997	Black Spruce, Canada <sup>c</sup>	-56	12
Baldocchi and others 1997	Jack Pine, Canada <sup>c</sup>	-47	4
Goulden and others 1998	Black Spruce, Canada <sup>a,c</sup>	-10 to +70	36
Black and others 1996	Aspen, Canada <sup>c</sup>	-130	12
Lindroth and others 1998	Norway spruce, Norunda, Sweden <sup>b</sup>	+60 to +90	24
Hollinger and others 1999	Spruce-hemlock, Maine, USA <sup>a</sup>	-210	12
Anthoni and others 1999	Ponderosa Pine, Oregon, USA <sup>a</sup>	-270 to -320	24

<sup>a</sup>AMERIFLUX.<sup>b</sup>EUROFLUX.<sup>c</sup>BOREAS.NEP: (-), uptake of CO<sub>2</sub>; (+), source of CO<sub>2</sub>.

the soil. Cao and Woodward (1998) and Kicklighter and others (1999) have suggested that the terrestrial biosphere will have a limited capacity to act as a sink of atmospheric CO<sub>2</sub> in the future as a result of physiological and nutrient constraints. Feedbacks and interactions among ecosystem processes with different response times are not well understood and are difficult to evaluate without long-term observations and, ideally, long-term experimental manipulations.

In a time frame of 50–200 years, several factors are likely to change the magnitude and direction of CO<sub>2</sub> exchange between terrestrial ecosystems and the atmosphere. Some of the important factors are: (a) changes in the frequency of fire and other large-area disturbances that lead to large, short-term C losses followed by a long, slow recovery of C stocks; (b) changes in plant species distributions and biome boundaries that may affect both C storage and C turnover over large areas (for example, the conversion of evergreen to deciduous forest or forest to grassland); and (c) losses of biodiversity and invasions by exotic species that may affect the efficiency of use and retention of C, N, and other elements, and water. Although we know these factors are potentially important, an integrated assessment is needed to evaluate their relative importance and interactions.

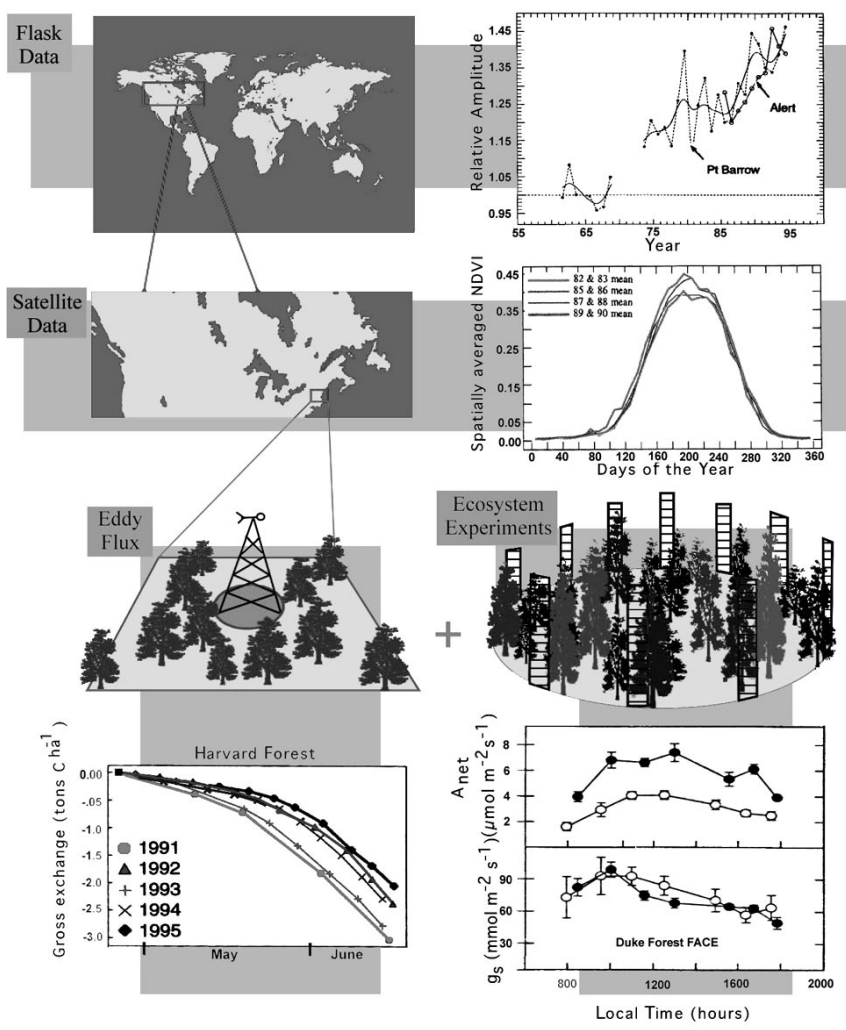
In addition, the Framework Convention for Climate Change and, more specifically, the recently

agreed on Kyoto Protocol, is attracting enormous interest from both the public and private sectors in managing and creating new terrestrial C sinks. The economic value of new sinks created by reforestation and afforestation, and the prospect of establishing a C trading system between industrial countries and less developing countries (that is, clean development mechanisms) have the prospect for affecting to some degree both the fluxes and stocks of C in terrestrial ecosystems.

## MULTITECHNIQUE APPROACH FOR IMPROVED UNDERSTANDING

Key questions for understanding the C metabolism of the terrestrial biosphere involve the spatial and temporal components of that metabolism. This includes the magnitude and phase of seasonal and interannual variability of C fluxes in individual biomes and the spatial variability within and among biomes. To address these two key issues, we need an integrated and multidisciplinary approach involving monitoring, experimentation, and modeling. An example of how such an integrated approach can be used is provided by explaining interannual variability in C fluxes realized by the study of measurements from the global air sampling network (Keeling and others 1996). An integrated suite of top-down measurements, including satellite data, eddy flux measurements, and ecosystem experiments,

### Measuring the Carbon Metabolism of the Biosphere



### Integration by Modeling

**Figure 3.** Measuring the carbon metabolism of the terrestrial biosphere. **Flask Data** (Air sampling network): Annual trend in the relative amplitude of atmospheric CO<sub>2</sub> at Point Barrow Alaska and Inert, Canada. The annual oscillation of CO<sub>2</sub> in northern latitudes has increased more than 40% since 1960 and has shifted 7 days earlier in the year (Keeling and others 1996). **Satellite Data**: NDVI averaged from 10-day maxima for 1982–83, 1985–86, 1987–88, and 1989–90. The satellite data indicate an advance of up to 7 days in the onset of the drawdown of atmospheric CO<sub>2</sub> in spring and early summer (Myneni and others 1997). **Eddy Flux**: Cumulative gross carbon exchange during spring for a deciduous forest in New England. In warmer years (1991 and 1993) leaves emerged 6–10 days earlier and increased gross carbon uptake by as much as 50% compared with cooler years (1992, 1994, and 1995; Goulden and others 1996a). **Ecosystem Experiments**: Diurnal pattern of net leaf photosynthesis ( $A_{net}$ ) and stomatal conductance ( $g_s$ ) for *Pinus taeda* trees in ambient and elevated CO<sub>2</sub> (open and closed symbols, respectively). Unlike many controlled environment studies, no decrease in leaf stomatal conductance was observed for trees grown 80 days in free-air CO<sub>2</sub> enrichment (FACE) (Ellsworth and others 1995).

can explain where and why interannual variability occurs (Figure 3). Satellite-based NDVI, for instance, might indicate earlier leaf-out in temperate and boreal forests (for example, Myneni and others 1997). Ground-based measurements of leaf area document the phenomenon locally, and tempera-

ture measurements yield its probable cause. Eddy flux then can be used to measure the consequences of earlier leaf-out on the annual C balance for the ecosystem (Wofsy and others 1993). Finally, ecosystem manipulative experiments (for example, elevated CO<sub>2</sub> and temperature experiments) can pro-

vide the mechanistic information necessary to model C fluxes under future global environmental scenarios.

Ecosystem process models, based on physiological principals, play an important role in scaling up to regional and global C metabolism. For the phenomenon of interannual variability, scenarios of temperature increase, atmospheric N deposition, land-use change, and accompanying changes in leaf phenology can be incorporated into models and examined for their effect on the components of the C budget and NEP.

Approaches of scaling down from global and continental measurements and scaling up from stand-level measurements both are critical for an integrative program of C research. The "top-down" approach locates the global and continental-scale C sources and sinks, whereas the "bottom-up" approach provides estimates of C fluxes at finer spatial scale and examines the mechanisms that control these fluxes at the scales of ecosystem, landscape, and region. Each approach has different spatial and temporal domains for which they offer information, and they have the potential to constrain the next level up or down.

## SCALING IN SPACE AND TIME

### Scaling Down

The long-term record of year to year changes of CO<sub>2</sub> concentration at Mauna Loa is an indirect indicator that C exchange between the terrestrial biosphere and atmosphere varies on a seasonal and annual basis (Keeling and others 1995; Figure 1). However, the measurement of atmospheric CO<sub>2</sub> concentration alone does not provide direct information on the magnitude of fluxes and the relative contribution of ecosystems, regions, or biomes.

New inverse modeling techniques can estimate C fluxes at the continental scale (Enting and others 1993; Fan and others 1998; Ciais and others 2000), although at present they are still at the exploratory stage. The inverse method uses CO<sub>2</sub> gradients among flask stations to resolve the fluxes spatially on a monthly basis over large regions of the globe. There are important shortcomings of this technique including questions as to how well the continents are constrained by the air sampling network and also limitations associated with the atmospheric transport models themselves, which are used in the calculations (Table 3). Despite these problems, the inverse method provides valuable first order spatial information on the location and strength of C sources and sinks of large areas of land and oceans,

and the technique is expected to improve greatly within the next few years.

Forward calculations using terrestrial biospheric process-based models is another approach to study the strength and spatial distribution of C sources and sinks in the terrestrial biosphere. They can be used for global estimates or scale down to any spatial resolution. Recent model intercomparisons, however, have shown the lingering limitations of these models in that they produce highly variable NPP and NEP results due to the various formulations and processes inherent in each model (Heimann and others 1998; Cramer and others 1999). One of the main barriers to rapid improvement of these models is the lack of ground data for validation purposes. However, several iterative and complementary methods can help models become more robust and realistic (Table 3): (a) model validation with scarce ground data; (b) aggregation of NEP model estimates using atmospheric transport models and comparison with CO<sub>2</sub> concentration measured from air sampling networks; (c) model intercomparisons with standard data sets to show the variety of formulations used and their implications for model outputs; and (d) further model development with new understanding generated by process-level studies.

### Scaling Up

The inverse method is a powerful tool for generating large-scale estimates that include all ecosystem processes and landscape components. However, this method does not provide much spatial resolution nor does it have the potential to increase our understanding of the terrestrial processes that control the fluxes. Therefore, ground-based approaches to study the dynamics of C sinks and sources are important and complementary to top-down approaches.

*Stand fluxes.* Considerable understanding has been gained from the study of leaf-level C fluxes and the extent that these fluxes can be scaled up. Multiyear eddy covariance measurements offer the capability of estimating NEP for a large area and are one of the most important approaches for studying ecosystem-level C fluxes. The greatest amount of insight is obtained from using both approaches simultaneously (Baldocchi and others 1996). Processes overlapping several years emerge from analyses of the interannual variability of CO<sub>2</sub> fluxes that would not be apparent from observing data from any single year. For example, Wofsy and others (1993) deduced from the comparison of the annual C budget of a whole stand in Harvard Forest over several years that interannual variability in both



**Table 3.** Available Approaches to Study the Carbon Cycle at Various Space and Time Scales

Approach	Strength	Weakness	Way to Improve It
Air sampling networks and inversion modeling	Global and continental scale C fluxes	Low regional resolution Poorly constrained No discrimination between C <sub>4</sub> vegetation and oceans	Extending air sampling networks including continental sites More scalars Use of δ <sup>13</sup> C and δ <sup>18</sup> O 3-D coverage
Satellite data	Global and regional estimates of leaf area and phenology	Algorithms have not been validated Intermittent coverage Indirect flux estimate	Acquire ground truth information from tower flux network and ground sampling New satellite platforms (EOS)
Terrestrial biospheric models	Spatial and temporal integration of process models Some use satellite data	Parameter intensive Not too realistic at large spatial scales Lack of data for validation	Validate with eddy flux network and other ground measurements Improve with process-level studies and experiments (for example, leaf phenology) Intermodel comparisons
Convective boundary layer measurements (aircraft, balloons, and tall towers)	Landscape scale information	Only daytime measurements Short term studies Theory still under development	Entrainment model Mixed layer scalar measurements
Stand-level flux networks (long-term eddy-covariance measurements)	Dynamic and process information Ecosystem scale (1 km <sup>2</sup> ) Continuous in time Excellent for model validation and development	Sensitivity to errors of nighttime fluxes Lack of mechanistic information Does not work on slopes Difficulty in partitioning photosynthesis and respiration	Isotopes and soil chambers yield information on compartments Collect ancillary information and process-level studies Extension of current network into new biomes
Ecosystem experiments	Provides process-level information Interactions among multiple drivers	Manipulation artifacts (for example, chamber effects) Short term	Appropriate controls Run for many years Emphasis on interactions Use model systems Use ecosystem models to better design experiments
Small cuvettes	Provides process-level information at leaf, stem, and soil scales	Poor spatial and temporal coverage Chamber effects	Fundamental physiological, soil, and microbial processes Mechanistic information

photosynthesis and respiration are associated with processes not well accounted for in classic ecophysiological models, such as leaf phenology and winter soil temperatures. Multiyear measurements also have shown that some ecosystems can shift from being a sink to a source of C (Oechel and others 1995; Goulden and others 1998). Thus, the use of interannual data resulting from long-term flux measurements will lead to the development and testing of models incorporating processes of the biosphere metabolism that are not currently well understood. Furthermore, tower NEP measurements offer unique

data sets for validation of both biospheric models and satellite products (for example, Earth Observing System).

A global network (FLUXNET) integrates ongoing and planned eddy covariance tower sites throughout the world. However, a majority of existing experimental sites currently are placed over temperate and boreal forests (Figure 2). This makes an extension into critical biomes, such as savannas, wetlands, major crops, subtropical and tropical forests, and arid lands, very important (Table 3). Better coverage of poorly represented ecosystems in con-

trasting climates will provide new combinations of environmental factors and controls over fluxes that will challenge models for more robust responses. Eddy flux studies also need to cover successional sequences of ecosystems, because the current distribution of sites focuses on mid-aged stands while ignoring more recently disturbed and older growth areas. Mobile eddy flux towers following stands in a chronosequence after disturbances (for example, fire, logging) could be used to study the fluxes associated with succession. Likewise, manipulative experiments (for example, N deposition, selected logging) in permanent tower sites is also an important application of eddy covariance.

**Regional fluxes.** Whereas a network of tower flux measurement provides dynamic information on ecosystem metabolism, these measurement systems are discrete in time and space. Hence, we will need to rely on a combination of flask sampling, satellite, and modeling information to derive an integrated global map that varies in time. The footprint of tower sites, which is on the order of 1 km<sup>2</sup>, may be scaled up with measurements of tropospheric CO<sub>2</sub> (S. Wofsy, personal communication), and so enhance the global flask network of CO<sub>2</sub> sampling that is positioned near oceanic sites (Tans and others 1996). Estimates of temporal changes of CO<sub>2</sub> in the convective boundary layer would provide an estimate of the regional C flux (Denmead and others 1996). Particularly, vertical CO<sub>2</sub> profiles of the convective boundary layer with tall towers (greater than 500 m) and aircrafts would greatly improve our understanding of C fluxes at the regional level (Bakwin and others 1995) and when appropriately modeled would allow us to scale up to larger regions. Increasing the spatial density of tropospheric CO<sub>2</sub> measurements also has the potential of improving upon the inverted estimates of C sources and sinks that are being provided by general circulation models (Tans and others 1990; Enting and others 1995; Denning and others 1996).

The combination of forest inventories with appropriate accounting of land-use change can help constraining and testing atmospheric measurements and model estimates (Houghton 1995, 1996, 1999). The technique can produce NPP and NEP estimates and has been applied at the regional scale (Kurz and Apps 1999). Unfortunately, traditional inventories often do not include all components of the system (for example, non-harvestable biomass, soil C) and they typically only cover forest systems, leaving a large portion of the terrestrial biosphere unaccounted.

**Stable isotopes and ancillary measurements.** Flux measurements at the stand level (eddy flux towers) and regional level (a combination of eddy flux tall

towers, balloons, and aircraft measurements) require additional studies to better understand processes that occur at multiple scales (soil, plants, and troposphere), so that appropriate methods for scaling up are used. For example, <sup>13</sup>C/<sup>12</sup>C-CO<sub>2</sub> ratios can provide information on the relative contribution at the regional-level of photosynthesis versus respiration because of the differential isotopic discrimination that occurs in each of these processes (Francey and Tans 1987). At the stand level, a combination of eddy flux towers, chamber-based measurements, and the analyses of changes in the stable isotope ratio of atmospheric CO<sub>2</sub> can provide adequate mechanistic information to properly interpret the larger scale fluxes (Baldocchi and others 1996). Stable isotopes (for example, <sup>13</sup>C Keeling plots) can also provide information on the relative flux contributions of various components of the system, such as soil, moss layer, and stems at the stand level (Flanagan and Ehleringer 1998). Carbon isotopes can also be used to assess the effects on C stocks and fluxes of replacing tropical forest (with C<sub>3</sub> photosynthetic system) with pasture (with C<sub>4</sub> photosynthetic system). C<sub>4</sub> plants have a lower carbon isotope discrimination during photosynthesis that allows for tracing of the new carbon inputs in the soil (Lloyd and Farquhar 1994).

Ecosystem processes also have an important effect on the oxygen isotopic ratio (<sup>18</sup>O/<sup>16</sup>O) of the atmospheric CO<sub>2</sub>. Photosynthesis and water diffusion between different compartments are the main sources of isotope discrimination and can differentiate above- and belowground respiratory sources. This has the potential for distinguishing among these sources at the ecosystem and regional scales. Recently, Flanagan and others (1997) working at the ecosystem level and Ciais and others (1997) working at the global level have applied the Farquhar model (Farquhar and others 1993) for oxygen isotope fractionation (<sup>18</sup>O/<sup>16</sup>O in CO<sub>2</sub>) to bridge ecosystem processes and global scales.

Flux measurements and isotope data will have to be taken concurrently with other important ancillary information on the state of the ecosystem. A list of such information would include climate conditions, soil moisture, soil physical and chemical properties, leaf area index, photosynthetic capacity, species composition, and biomass allocation into different components (see Baldocchi and others 1996). For example, chamber flux and biomass measurements together provide information on how C is allocated to different vegetation components (wood, foliage, fine roots), which decompose at very different rates. The allocation of large amounts of C to fine roots in cold soils may decouple C

assimilation and decomposition, resulting in C accumulation in the soil (Jackson and others 1997; Steele and others 1997).

*Integration by modeling.* Spatial scales represented by the different relevant measurements vary widely, from a single leaf measured by physiological studies, to a few hectares sampled by flux towers, to a few hundred kilometers sampled by aircraft and balloons, finally to global coverage of satellite data. Each of these measurements also has a defined temporal sampling frequency. Flux towers measure CO<sub>2</sub> every few minutes whereas the flask network measures CO<sub>2</sub> only monthly. It is the role of biospheric models to help to synthesize these disparate time/space data into a single coherent analysis of the terrestrial C metabolism. There is also the need, however, to design measurement protocols to best couple the step scales used in models. For example, a specific measurement gap exists between the local measurements of the flux tower and air sampling network's "bottom-up perspective" and the global satellite's "top-down" perspective. Politically essential national boundaries are defined at this regional to continental scale, and biospheric models are required to accurately resolve these scales of terrestrial C metabolism (VEMAP 1995).

### Scaling in Time

*Manipulative experiments.* It is unlikely that ecosystem responses to annual climatic variation or short-term climate trends will give an unambiguous indication of the magnitude of longer-term changes in C fluxes. Critical controls of C fluxes such as climate, atmospheric CO<sub>2</sub> and N are changing and will continue to change over the next century. For example, the immediate effect of warming may be to increase NPP through increased photosynthesis. However, in the longer-term the uptake and accumulation of N in plant biomass (particularly in forests) may reduce soil N availability and, hence, the possibility for further increases in NPP. A recent synthesis of experiments showed that some of the current model assumptions on the effects of elevated CO<sub>2</sub> are not correct (Mooney and others 1999). For instance, stomatal conductance decreased consistently in grasslands and deciduous trees growing in rich CO<sub>2</sub> atmosphere whereas stomatal conductance did not change in mature conifer trees. The whole time sequence of multiple responses to environmental change can be captured only in long-term manipulative experiments (greater than 10 years).

In addition, multiple drivers of global change will interact showing positive and negative responses, sometimes on the same ecosystem process. For

instance, although warming may decrease soil moisture, elevated atmospheric CO<sub>2</sub> decreases stomatal conductance in many systems, which enhances soil moisture (Field and others 1996). Thus, multifactorial experiments are critical to understand the interactive nature of global environmental change (Table 3).

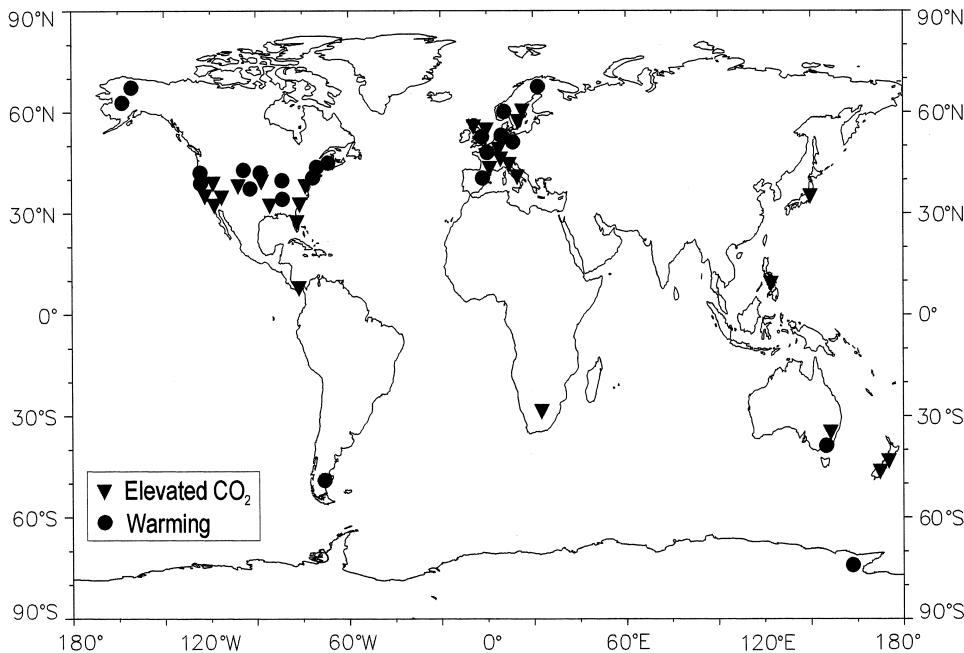
Choice of experiment location should maximize the range of environmental conditions and ecosystem types under study. The current distribution of ecosystem experiments is highly concentrated in temperate and boreal environments (Figure 4). However, the selection of "model ecosystems" is also desirable. Model ecosystems are chosen not necessarily for their representativeness but because they contribute to the understanding of the principles that regulate ecosystem responses. They usually have accelerated dynamics and are easy to manipulate and work with (Field and others 1996). For instance, systems that contain plants with short life cycles (for example, annual grasses) can have several plant generations during the span of one experiment, thereby allowing for changes in community dynamics and associated changes in physiology and biogeochemistry in response to manipulations.

There are a variety of other complementary tools that can be used to study the mechanisms involved in future trajectories of the terrestrial C fluxes. Vegetation around naturally occurring CO<sub>2</sub> springs offers great opportunities to study intact systems that have been growing under elevated CO<sub>2</sub> conditions for hundreds of years (Hättenschwiler and others 1997). Likewise, the substitution of space for time in selected temperature and precipitation gradients can lead to many insights, especially when combined with experiments (for example, species and plot removal experiments).

The experimental challenge is to provide the fundamental mechanistic and process-level understanding to develop and validate models with the prognostic capacity to predict future ecosystem functioning. Likewise, process models will help to design the appropriate experiments to test current model formulations or to introduce critical processes that currently are not taken into account in the models. By doing so, we will create a bidirectional iterative feedback between experiments and models for improving our predictive capability.

### Landscape and Regional Disturbances

In addition to changes in climate, atmospheric CO<sub>2</sub>, and N deposition, there are factors that have the potential to change not only the magnitude but also the sign of currently observed ecosystem fluxes within the next one or two centuries. These are



**Figure 4.** Networks of ecosystem experiments on elevated  $\text{CO}_2$  (▼) [for example, Free Air Carbon Dioxide Enrichment (FACE), open-top chambers] and elevated temperature (●) (for example, soil buried cables, infrared radiators, passive greenhouses, open-top chambers) coordinated by GCTE core project of the IGBP.

factors such as (a) changes in the frequency of large-scale disturbances, (b) changes in species distributions and biome boundaries, and (c) losses of biodiversity and invasions by exotic species. Changes in biome distribution are accounted in DGVMs of potential vegetation, and some also include disturbance regimes, mostly fire. Terrestrial biogeochemistry models and other models do not account for disturbances nor biological invasions both of which are known to have large impacts on ecosystem fluxes. For instance, forest ecosystems in Canada have decreased their C sink strength during the 1980s due exclusively to an increase of disturbances—mainly wildfires and insect attacks (Kurz and Apps 1999).

Multiyear eddy covariance measures at the stand level and short-term measurement of the convective boundary layer do not account for the effect of disturbance at the landscape scale. Disturbances involving rapid changes of C stocks in ecosystems include natural phenomena (fire, hurricanes, landslides, floods, insect attacks), as well as human activities (land clearing for agriculture or pasture, timber harvesting). For example, burning of a forest stand involves rapid transfer of C built up over many years in soils and biomass back to the atmosphere. After disturbance, C often is sequestered at a changing rate as vegetation regrowth progresses throughout several successional stages (Gower and others 1996; Ryan and others 1997). An integrated approach expanding to larger spatial and longer temporal scales will have to take into account the net effects of the burning/regrowth cycle and

changes of the frequency and nature of this cycle due to climate change (Piñol and others 1998; Kurz and Apps 1999) and landscape fragmentation. Terrestrial biosphere models must couple disturbance and ecosystem process models to simulate the effects of land-use change on ecosystem processes and C exchange between the terrestrial biosphere and atmosphere.

Climatic variability, such as ENSO events, may cause interannual variations in C storage through physiological responses to temperature and precipitation (Tian and others 1998). Furthermore, fire frequency is higher in regions affected by increased ENSO-related drought and logging practices throughout Amazonia (Nepstad and others 1999). Similarly, future climatic change will manifest itself both through changes in mean annual conditions and through frequency and intensity of extreme events, such as fires and hurricanes. We do not know the relative importance of these two types of responses at the global scale.

## SUMMARY

The C dynamics of the terrestrial biosphere are complex. Understanding these dynamics in detail is vitally important because the terrestrial biosphere plays a major role in the global C cycle, and because humans have measurably perturbed the C cycle in ways that will not only alter the climate system but also will directly affect terrestrial metabolism. In fact, changes in terrestrial metabolism may well be



as important an indicator of global change as the changing temperature signal.

Presently, we use a large array of tools to help us understand the C cycle. Each of these tools provides a piece of the C balance puzzle, but there is no single approach that gives us the total spatial and temporal resolution that is needed to understand global, regional, and local C dynamics. Thus, as we move forward in understanding terrestrial C metabolism, we need an integrated approach that incorporates the various tools that have been developed. We also need a better way of making sure that we are getting all of the necessary information while avoiding redundancy of effort.

As we prepare to implement the Kyoto Protocol, agreed to by the parties of the FCCC to slow down increases of atmospheric CO<sub>2</sub>, nations will need precise information on the variability of background levels of C exchange of their biotic systems, and on how humans are modifying these exchanges. Furthermore, there is the need to critically analyze, under the allowances of the Kyoto Protocol, the potential long-term impact of managing terrestrial C sinks on the global C cycle, particularly in the context of longer term dynamics of ecosystems.

Meeting these challenges will require a concerted effort at the international level to assess what we currently understand about the dynamics of the C cycle and to improve that understanding through ongoing research. At present, nations depend on the Intergovernmental Panel on Climate Change (IPCC), an international team of interdisciplinary scientists, to assess information available on the C cycle and on other elements influencing climate change. The IPCC, sponsored by the World Meteorological Organization and the United Nations Environment Program, does not direct or coordinate research but summarizes available information and notes the policy relevance of the findings. The research input that is utilized comes from the normal undirected scientific process, although some nations currently are developing integrative C research programs.

At the international level, no program has examined, and more importantly, coordinated C cycle research among the multiple initiatives and disciplines dealing with individual components of the carbon cycle. Recently, however, the International Geosphere-Biosphere Program (IGBP) has initiated a coordinated research effort on the C cycle that complements and adds value to undirected research and to programs being developed at national and regional levels. The IGBP carbon cycle program is built on core research projects that deal with parts of C metabolism, including C dynamics of the ocean, response of terrestrial ecosystems to global change,

and modeling the earth system. This program currently is undertaking a synthesis to improve our understanding of the dynamics of the C cycle based on current and past work, and building an explicit framework for coordinating future C cycle research across disciplines, scales, and countries/regions. Collaboration with the partner international programs, WCRP (World Climate Research Program) and IHDP (International Human Dimensions Program on Global Environmental Change), addresses additional aspects of C cycle research, such as the two-way coupling between the physical climate system and the C cycle and the socioeconomic and political aspects of attempts to manage parts of the C cycle.

International coordination will be critical as we try to understand global C metabolism, the drivers of change, and the potential role of managing our terrestrial biosphere.

## ACKNOWLEDGMENTS

This article contributes to the GCTE Terrestrial Carbon Initiative and IGBP Carbon Working Group. We are thankful to Richard Houghton and Kathy Hibbard for providing useful comments to this manuscript. We also thank the support of the National Aeronautics and Space Administration (NASA-USA) and the Australian Greenhouse Office (AGO-Australia) to GCTE through the funding of the GCTE Focus 1 Office in the USA and the GCTE International Project Office in Australia, respectively.

## REFERENCES

- Anthoni PM, Law BE, Unsworth MH. 1999. Carbon and water exchange of an open-canopied ponderosa pine ecosystem. *Agricult For Meteorol* 95:151-68.
- Bacastow RB. 1976. Modulation of atmospheric carbon dioxide by the southern oscillation. *Nature* 261:116-8.
- Bakwin PS, Tans PP, Zhao C, Ussler W, Quesnell E. 1995. Measurements of carbon dioxide on a very tall tower. *Tellus* 47B:535-49.
- Baldocchi D, Valentini R, Running S, Oechel W, Dahlman R. 1996. Strategies for measuring and modelling carbon dioxide and water vapour fluxes over terrestrial ecosystems. *Global Change Biol* 2:159-68.
- Baldocchi DD, Vogel CA, Hall B. 1997. Seasonal-variation of energy and water-vapor exchange-rates above and below a boreal jack pine forest canopy. *J Geophys Res Atmospheres* 102:28939-51.
- Belward A. 1996. The IGBP-DIS Global 1km Land Cover Data Set. Proposal and implementation plans. International Geosphere-Biosphere Program-Data and Information System working paper 13, Toulouse.
- Black TA, den Hartog G, Neumann HH, Blanken PD, Yang PC, Russell C, Nestic Z, Lee X, Chen SG, Staebler R, Novak MD. 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. *Global Change Biol* 2:219-30.

- Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze E-D. 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108:583-95.
- Cao M, Woodward FI. 1998. Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature* 393:249-52.
- Ciais P, Tans PP, Trolier M, White JWC, Francey RJ. 1995. A large Northern Hemisphere terrestrial CO<sub>2</sub> sink indicated by the <sup>13</sup>C/<sup>12</sup>C ratio of atmospheric CO<sub>2</sub>. *Science* 269:1098-102.
- Ciais P, Denning AS, Tans PP, Berry JA, Randall DA, Collatz GJ, Sellers PJ, White JWC, Trolier M, Meijer HJ, Francey RJ, Monfray PM, Heimann M. 1997. A three dimensional synthesis study of <sup>18</sup>O in atmospheric CO<sub>2</sub>. Part 1: surface fluxes. *J Geophys Res* 102:5857-72.
- Ciais P, Peylin P, Bousquet P. 2000. The regional distribution of the biospheric carbon fluxes as inferred from atmospheric CO<sub>2</sub> measurements and models. *Ecol Appl*. Forthcoming.
- Conway TJ, Tans PP, Waterman LS. 1994. Atmospheric CO<sub>2</sub> records from sites in the NOAA/CMDL air sampling network. In: Boden TA, Kaiser DP, Sepanski RJ, Stoss FW, editors. *Trends '93: a compendium of data on global change*. ORNL/CDIAC-65. Oak Ridge, TN: Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, pp 62-119.
- Cramer W, Kicklighter DW, Bondeau A, Moore B III, Churkina G, Nemry B, Ruimy A, Schloss AL, and the Participants of Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biol* 5:1-15.
- Denmead OT, Raupach MR, Dunin FX, Cleugh HA, Leuning R. 1996. Boundary-layer budgets for regional estimates of scalar fluxes. *Global Change Biol* 2:255-64.
- Denning AS, Collatz GJ, Zhang C, Randall DA, Berry JA, Sellers P, Colello GD, Dazlich DA. 1996. Simulations of terrestrial carbon metabolism and atmospheric CO<sub>2</sub> in a general circulation model. Part 1: surface carbon fluxes. *Tellus Ser B Chem Phys Meteorol* 48:521-42.
- Ellsworth DS, Oren R, Huang C, Phillips N, Hendrey GR. 1995. Leaf and canopy responses to elevated CO<sub>2</sub> in a pine forest under free-air CO<sub>2</sub> enrichment. *Oecologia* 104:139-46.
- Enting IG, Trudinger CM, Francey RJ, Granek H. 1993. Synthesis inversion of atmospheric CO<sub>2</sub> using the GISS tracer transport model. *CSIRO Aust Div Atmos Res Tech Paper* 29:1-44.
- Enting IG, Trudinger CM, Francey RJ. 1995. A synthesis inversion of the concentration and delta-<sup>13</sup>C of atmospheric CO<sub>2</sub>. *Tellus Ser B Chem Phys Meteorol* 47:35-52.
- Fan S, Gloor M, Mahlman J, Pacala S, Sarmiento J, Takahashi T, Tans P. 1998. A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. *Science* 282:442-6.
- Farquhar GD, Lloyd J, Taylor JA, Flanagan LB, Syvertsen JP, Hubick KT, Wong CS, Ehleringer JR. 1993. Vegetation effects on the isotope composition of oxygen and atmospheric CO<sub>2</sub>. *Nature* 363:439-43.
- Field CB, Chapin FS III, Chiariello NR, Holland EA, Mooney HA. 1996. The Jasper Ridge CO<sub>2</sub> experiment: design and motivation. In: Koch G, Mooney HA, editors. *Carbon dioxide and terrestrial ecosystems*. San Diego, CA: Academic Press. p 121-45.
- Flanagan LB, Ehleringer JR. 1998. Ecosystem-atmosphere CO<sub>2</sub> exchange: interpreting signals of change using stable isotope ratios. *Trends Ecol Evol* 13:10-4.
- Flanagan LB, Brooks JR, Varney GT, Ehleringer JR. 1997. Discrimination against C<sup>18</sup>O<sup>16</sup>O during photosynthesis and the oxygen isotope ratio of respired CO<sub>2</sub> in boreal ecosystems. *Global Biogeochem Cycles* 11:83-98.
- Foley JA, Prentice IC, Ramankutty N, Levis S, Pollard D, Sitch S, Haxeltine A. 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. *Global Biogeochem Cycles* 10:603-28.
- Francey RJ, Tans PP. 1987. Latitudinal variation in oxygen-18 of atmospheric CO<sub>2</sub>. *Nature* 327:495-7.
- Fung IY, Tucker CJ, Prentice KC. 1987. Application of advanced very high resolution radiometer vegetation index to study atmosphere-biosphere exchange of CO<sub>2</sub>. *J Geophys Res* 92:2999-3015.
- Goulden JL, Munger JW, Fan S-M, Daube BC, Wofsy SC. 1996a. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* 271:1576-8.
- Goulden ML, Munger W Jr, Fan S-M, Daube BC, Wofsy SC. 1996b. Measurements of carbon sequestration by long-term eddy covariance methods and a critical evaluation of accuracy. *Global Change Biol* 2:169-82.
- Goulden ML, Wofsy SC, Harden JW, Trumbore SE, Crill PM, Gower ST, Fries T, Daube BC, Fan SM, Sutton DJ, Bazzaz A, Munger JW. 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* 279:214-7.
- Gower ST, McMurtrie RE, Murty D. 1996. Aboveground net primary production decline with stand age: potential causes. *Trends Ecol Evol* 11:378-82.
- Grace J, Lloyd J, McIntyre J, Miranda A, Meier P, Miranda H, Moncrieff J, Massheder J, Whright I, Gash J. 1995. Fluxes of carbon dioxide and water vapour over an undisturbed tropical forest in south-west Amazonia. *Global Change Biol* 1:1-12.
- Greco S, Baldocchi DD. 1996. Seasonal variations of CO<sub>2</sub> and water vapour exchange rates over a temperate deciduous forest. *Global Change Biol* 2:183-98.
- Hättenschwiler S, Miglietta F, Raschi A, Körner Ch. (1997). In situ forest tree growth over a 30-year period in naturally CO<sub>2</sub>-enriched atmospheres. *Global Change Biol* 3:463-71.
- Heimann M, Esser G, Haxeltine A, Kaduk J, Kicklighter DW, Knorr W, Kohlmaier GH, McGuire AD, Melillo J, Moore B III, and others. 1998. Evaluation of terrestrial carbon cycle models through simulations of the seasonal cycle of atmospheric CO<sub>2</sub>: first results of a model intercomparison study. *Global Biogeochem Cycles* 12:1-24.
- Holland EA, Braswell BH, Lamarque J-F, Townsend A, Sulzman J, Muller J-F, Dentener F, Brasseur G, Levy II H, Penner JE, Roelofs G-J. 1997. Variations in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems. *J Geophys Res* 102:15849-66.
- Hollinger DY, Goltz SM, Davidson EA, Lee JT, Tu K, Valentine HT. 1999. Seasonal patterns and environmental control of carbon dioxide and water vapor exchange in an ecotonal boreal forest. *Global Change Biol*. 5:891-902.
- Houghton RA. 1990. The global effects of tropical deforestation. *Environ Sci Technol* 24:414-22.
- Houghton RA. 1995. Land-use change and the carbon cycle. *Global Change Biol* 1:275-87.
- Houghton RA. 1996. Terrestrial sources and sinks of carbon inferred from terrestrial data. *Tellus Sers B, Chem Phys Meteorol* 48:420-32.
- Houghton RA. 1999. The annual net flux of carbon to the atmosphere from changes in land use 1850-1990. *Tellus* 51B:298-313.

- Houghton RA, Hackler JL. 1999. Emissions of carbon from forestry and land-use change in tropical Asia. *Global Change Biol* 5:481–92.
- Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze E-D. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108:389–411.
- Jackson RB, Mooney HA, Schulze E-D. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proc Natl Acad Sci USA* 94:7362–6.
- Jarvis PG, Massheder JM, Hale SE, Moncrieff JB, Rayment M, Scott SL. 1997. Seasonal-variation of carbon-dioxide, water-vapor, and energy exchanges of a boreal black spruce forest. *J Geophys Res Atmospheres* 102:28953–66.
- Jobbagy EG, Jackson RB. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol Appl*. Forthcoming.
- Keeling CD, Whorf TP. 1998. Atmospheric CO<sub>2</sub> records from sites in the SIO air sampling network. In: Trends: a compendium of data on global change. Oak Ridge, TN: Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory.
- Keeling CD, Whorf TP, Wahlen M, Van der Plicht J. 1995. Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* 375:666–70.
- Keeling CD, Chin JFS, Whorf TP. 1996. Increased activity of northern vegetation inferred from atmospheric CO<sub>2</sub> measurements. *Nature* 382:146–9.
- Kicklighter DW, Bruno M, Dönges S, Esser G, Heimann M, Helfrich J, Ift F, Joos F, Kaduk J, Kohlmaier GH, and others. 1999. A first-order analysis of the potential role of CO<sub>2</sub> fertilization to affect the global carbon budget: a comparison of four terrestrial biosphere models. *Tellus* 51B:343–66.
- Knorr W, Heimann M. 1995. Impact of drought stress and other factors on seasonal land biosphere CO<sub>2</sub> exchange studied through an atmospheric tracer transport model. *Tellus* 47B:471–89.
- Kurz WA, Apps MJ. 1999. A 70-yr retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecol Appl* 9:526–47.
- Lindroth A, Grelle A, Morén A-S. 1998. Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity. *Global Change Biol* 4:443–50.
- Lloyd J, Farquhar GD. 1994. <sup>13</sup>C discrimination during CO<sub>2</sub> assimilation by the terrestrial biosphere. *Oecologia* 99:201–15.
- Mack F, Hoffstadt J, Esser G, Goldammer JG. 1996. Modeling the influence of vegetation fires on the global carbon cycle. In: Levine JS, editor. Biomass burning and global change. Cambridge, MA: The MIT Press. p 149–59.
- Matthews E. 1997. Global litter production, pools, and turnover times: Estimates from measurements data and regression models. *J Geophys Res-Atmos* 102:18771–18800.
- Melillo JM, McGuire A, Kicklighter D, Moore B III, Vorosmarty C, Schloss A. 1993. Global climate change and terrestrial net primary production. *Nature* 363:234–40.
- Mooney H, Canadell J, Chapin FS, Ehleringer J, Körner Ch, McMurtrie R, Parton W, Pitelka L, Schulze D-E. 1999. Ecosystem physiology responses to global change. In: Walker BH, Steffen WL, Canadell J, Ingram JSI, editors. The terrestrial biosphere and global change: implications for natural and managed ecosystems. London: Cambridge University Press. p 141–89.
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386:698–702.
- Nemani R, Running SW. 1996. Implementation of a hierarchical global vegetation classification in ecosystem function models. *J Vegetation Sci* 7:337–46.
- Nepstad DC, Verissimo A, Alencar A, Nobres C, Lima E, Lefebvre P, Schlesinger P, Potter C, Mounthiho P, Mendoza E, Cochrane M, Brooks V. 1999. Large-scale impoverishment of Amazonian forests by logging and fire. *Nature* 398:505–8.
- Oechel WC, Vourlitis GL, Hastings SJ, Bochkarev SA. 1995. Change in arctic CO<sub>2</sub> flux over two decades: effects of climate change at Barrow, Alaska. *Ecol Appl* 5:846–55.
- Piñol J, Terradas J, Lloret F. 1998. Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. *Climate Change* 38:345–57.
- Post WM, Emanuel WR, Zinke PJ, Stangenberger AG. 1982. Soil carbon pools and world life zones. *Nature* 317:613–6.
- Prentice IC. 1990. Bioclimatic distribution of vegetation for general circulation model studies. *J Geophys Res* 95:11811–30.
- Running SW, Baldocchi DD, Cohen W, Gower ST, Turner D, Bakwin P, Hibbard K. 1999. A global terrestrial monitoring network integrating fluxes, flask sampling, ecosystem modeling and EOS satellite data. *Remote Sens Environ* 70:180–187.
- Ryan MG, Binkley D, Fownes JH. 1997. Age-related decline in forest productivity: pattern and process. *Adv Ecol Res* 27:213–62.
- Schimel DS, Alves D, Enting I, Heimann M, Joos F, Raynaud D, Wigley T, Prather M, Derwent R., Ehhalt D, and others 1996. Radiative forcing of climate change. In: Houghton JT, Filo LGM, Callander BA, Harris N, Kattenberg A, Maskell K, editors. Climate change 1995. The science of climate change. Cambridge, UK: Cambridge University Press. p 65–131.
- Scurlock JMO, Cramer W, Olson RJ, Parton WJ, Prince SD, Members G. 1999. Terrestrial NPP: towards a consistent data set for global model evaluation. *Ecol Appl* 9:913–19.
- Sproles DW. 1996. The development of a global biomass burning inventory. In: Levine JS, editor. Biomass burning and global change. Volume 1. Cambridge, MA: MIT Press. p 202–22.
- Steele SJ, Gower ST, Vogel JG, Norman JM. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. *Tree Physiol* 17:577–87.
- Tans PP, Fung IY, Takahashi T. 1990. Observational constraints on the global atmospheric carbon dioxide budget. *Science* 247:1431–43.
- Tans PP, Bakwin PS, Guenther DW. 1996. A feasible global carbon-cycle observing system: a plan to decipher today's carbon-cycle based on observations. *Global Change Biol* 2:309–18.
- Taylor JA, Lloyd J. 1992. Sources and sinks of atmospheric CO<sub>2</sub>. *Aust J Bot* 40:407–18.
- Thompson MV, Randerson JT, Malmstrom CM, Field CB. 1996. Change in net primary production and heterotrophic respiration: how much is necessary to sustain the terrestrial carbon sink? *Global Biogeochem Cycles* 10:711–26.
- Tian H, Melillo JM, Kicklighter DW, McGuire AD, Helfrich JVK III, Moore B III, Vörösmarty CJ. 1998. Effect of interannual climate variability on carbon storage in Amazonian Ecosystems. *Nature* 396:664–7.
- Tucker CJ, Fung IY, Keeling CD, Gammon RH. 1986. Relationship between atmospheric CO<sub>2</sub> variations and a satellite-derived vegetation index. *Nature* 319:195–9.
- Valentini R, Deangelis P, Matteucci G, Monaco R, Dore S, Mugnozza GES. 1996. Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. *Global Change Biol* 2:199–208.

VEMAP Members. 1995. Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO<sub>2</sub> doubling. *Global Biogeochem Cycles* 9:407-38.

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997. Human domination of Earth's ecosystems. *Science* 277:494-9.

Walker BH, Steffen WL, Canadell J, Ingram JSI, editors. 1999. *The terrestrial biosphere and global change: implications for natural and managed ecosystems*. London: Cambridge University Press.

Wofsy SC, Goulden ML, Munger JW, Fan S-M, Bakwin PS, Daube BC, Bassow SL, Bazzaz FA. 1993. Net exchange of carbon dioxide in a mid-latitude forest. *Science* 260:1314-7.