

Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems

D. S. Schimel^{1,2†}, J. I. House¹, K. A. Hibbard², P. Bousquet³, P. Ciais³, P. Peylin⁴, B. H. Braswell¹³, M. J. Apps⁵, D. Baker⁶, A. Bondeau⁷, J. Canadell⁸, G. Churkina¹, W. Cramer⁷, A. S. Denning⁹, C. B. Field¹⁰, P. Friedlingstein³, C. Goodale¹⁰, M. Heimann¹, R. A. Houghton¹¹, J. M. Melillo¹², B. Moore III¹³, D. Murdiyarso¹⁴, I. Noble¹⁵, S. W. Pacala¹⁶, I. C. Prentice¹, M. R. Raupach¹⁷, P. J. Rayner¹⁸, R. J. Scholes¹⁹, W. L. Steffen²⁰ & C. Wirth¹

Knowledge of carbon exchange between the atmosphere, land and the oceans is important, given that the terrestrial and marine environments are currently absorbing about half of the carbon dioxide that is emitted by fossil-fuel combustion. This carbon uptake is therefore limiting the extent of atmospheric and climatic change, but its long-term nature remains uncertain. Here we provide an overview of the current state of knowledge of global and regional patterns of carbon exchange by terrestrial ecosystems. Atmospheric carbon dioxide and oxygen data confirm that the terrestrial biosphere was largely neutral with respect to net carbon exchange during the 1980s, but became a net carbon sink in the 1990s. This recent sink can be largely attributed to northern extratropical areas, and is roughly split between North America and Eurasia. Tropical land areas, however, were approximately in balance with respect to carbon exchange, implying a carbon sink that offset emissions due to tropical deforestation. The evolution of the terrestrial carbon sink is largely the result of changes in land use over time, such as regrowth on abandoned agricultural land and fire prevention, in addition to responses to environmental changes, such as longer growing seasons, and fertilization by carbon dioxide and nitrogen. Nevertheless, there remain considerable uncertainties as to the magnitude of the sink in different regions and the contribution of different processes.

A proportion of the carbon dioxide emitted to the atmosphere by fossil-fuel burning and terrestrial processes (mainly deforestation) is taken up by the oceans and the terrestrial biosphere. High-precision atmospheric observations of concentrations of CO₂ and O₂ (as O₂:N₂ ratios) make it possible to partition the uptake of atmospheric CO₂ between the land and ocean with increased confidence^{1–3}. Global carbon budgets have been updated in the most recent IPCC assessment⁴ using this approach (Table 1). The net terrestrial biospheric flux between the land and atmosphere was about –0.2 gigatonnes of carbon per year (Gt C yr^{–1}) in the 1980s and –1.4 Gt C yr^{–1} in the 1990s (the negative sign denotes a flux from the atmosphere). The net terrestrial biospheric flux is the difference between terrestrial uptake (sinks) and sources. Estimates of land-use change suggest emissions in the range of +0.6 to +2.5 Gt C yr^{–1} for the 1980s, largely from deforestation in the tropics⁴. If emissions due to land-use change were of a similar magnitude in the 1990s, this would imply a residual terrestrial sink of between about –2 and –4 Gt C yr^{–1}.

Spatial patterns of carbon uptake

Over the past two decades, evidence has accumulated of significant contributions of extratropical Northern Hemisphere land areas to the global uptake of anthropogenic CO₂: this evidence has been obtained from analysis of land inventory data^{5–8}, atmospheric CO₂ data^{9–13}, atmospheric O₂ data^{1–3}, isotopic analyses^{3,14}, studies of land-use change¹⁵ and ecosystem process models^{16,17}. Figure 1 shows zonal flux estimates from an ensemble of global atmospheric inverse model calculations: this is a method that back-calculates

sources and sinks of CO₂ from the distribution of atmospheric concentrations, resulting in a range of estimates of the northern extratropical net land sink from –0.6 to –2.3 Gt C yr^{–1} in the 1980s¹³.

Broad longitudinal partitioning of fluxes remains less certain than broad latitudinal partitioning, mainly because the former give rise to smaller differences in concentration^{14,18}. Inverse model results are highly sensitive to the subset of atmospheric data used, to the spatial and temporal resolution of the calculation method, and to the atmospheric model used¹², as indicated in Table 2. For example, the estimates of the North American sink range from 0 to 88% of the total northern land sink, depending on the approach.

Recent inverse modelling studies of the northern extratropical sink do not indicate a large imbalance of fluxes between North

Table 1 Contemporary carbon budgets for the 1980s and 1990s

	1980s* (Gt C yr ^{–1})	1990s* (Gt C yr ^{–1})
Emissions (fossil-fuel burning, cement manufacture)	5.4 ± 0.3	6.3 ± 0.4
Atmospheric increase	3.3 ± 0.1	3.2 ± 0.1
Ocean–atmosphere flux	–1.9 ± 0.5	–1.7 ± 0.5
Land–atmosphere flux	–0.2 ± 0.7	–1.4 ± 0.7
Emissions due to land-use change	1.7 (0.6 to 2.5)†	Assume 1.6 ± 0.8‡
Residual terrestrial sink	–1.9 (–3.8 to 0.3)	–2 to –4 (Highly uncertain)

Negative values denote flux from the atmosphere, that is, ocean or land uptake.

* From ref. 4.

† The range of estimates available to IPCC 2001 (ref. 4).

‡ Based on the early 1990s only and not the full decade (ref. 24).

¹ Max Planck Institute für Biogeochemie, Jena, Germany; ² IGBP/GAIM, University of New Hampshire, Morse Hall, Durham, New Hampshire 03824, USA; ³ LSCE Unité mixte CEA-CNRS, Bat. 709, CE L'Orme des Merisiers, 91191, Gif sur Yvette France; ⁴ Laboratoire de Biogéochimie Isotopique, Unité mixte CNRS-UPMC-INRA, 4 Place Jussieu, 75252 Paris, France; ⁵ Natural Resources Canada, Canadian Forest Service Northern Forestry Center, 5320 122 Street, Edmonton, Alberta, Canada; ⁶ NCAR, 1850 Table Mesa Drive, Boulder 80303, USA; ⁷ Potsdam Institute for Climate Impact Research, Telegrafenberg C4, 14473 Potsdam; ⁸ GCTE International Project Office, CSIRO Sustainable Ecosystems, PO Box 284, Canberra, ACT 2601, Australia; ⁹ Department of Atmospheric Science, Colorado State University, Fort Collins, Colorado 80523-1371, USA; ¹⁰ Carnegie Institution of Washington, Department of Plant Biology, 260 Panama Street, Stanford, California 94305, USA; ¹¹ Woods Hole Research Center, PO Box 296, Woods Hole, Massachusetts 02543, USA; ¹² Ecosystems Center, Marine Biological Laboratory, Woods Hole,

Massachusetts 02543, USA; ¹³ University of New Hampshire, Institute for the Study of Earth, Oceans and Space, Durham, New Hampshire 03824, USA; ¹⁴ GCTE Impacts Center for Southeast Asia, Jalan Raya Tajur Km 6, POB 116, Bogor, Indonesia; ¹⁵ Ecosystem Dynamics, RSBS, Australian National University, POB4 Acton, Canberra, ACT 0200, Australia; ¹⁶ Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Hampshire 08544-1003, USA; ¹⁷ CSIRO Division of Land and Water, GPO Box 1666, Canberra ACT 2601, Australia; ¹⁸ CSIRO-DAR, PMB #1, 3195 Aspendale, Australia; ¹⁹ Environmentek, CSIR, PO Box 395, Pretoria 0001, South Africa; ²⁰ IGBP Secretariat, Box 50005, S104-05, Stockholm, Sweden.

²¹ Present address: National Center for Atmospheric Research, 1850 Table Mesa Drive, Boulder, Colorado 80305, USA.

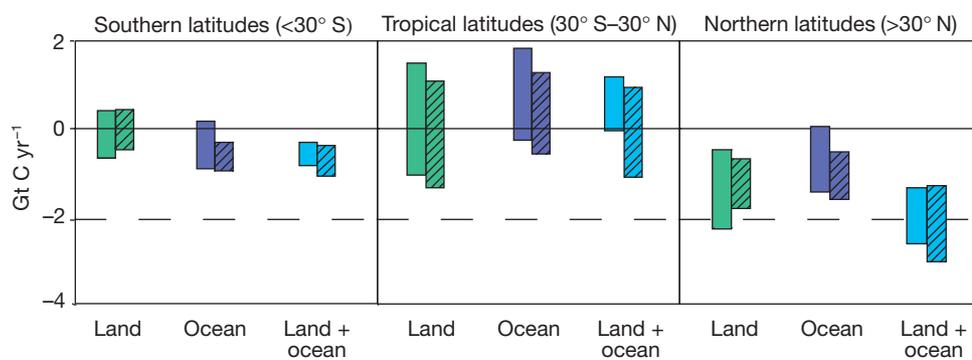


Figure 1 Zonal distribution of terrestrial and oceanic carbon fluxes. These data were deduced from eight inverse models using different techniques and sets of atmospheric observations after accounting for fossil-fuel emissions (not shown)¹³. Results are shown for the 1980s (plain bars) and for 1990–96 (hatched bars). The bars indicate

the full range of results from the models. Positive numbers are fluxes to the atmosphere. Note that data and time-intervals are not precisely consistent with those used in other analyses presented in this Progress Article, and so the global totals may differ from those mentioned elsewhere.

America and Eurasia^{3,11,12,19–21}, in contrast to earlier reports of a dominant sink in North America²². Given the controversy over the east–west partitioning of sinks, we need to consider if there is a biophysical or climatic reason to expect North America and Eurasia to differ greatly in ecosystem carbon uptake. Although the mean of the results in Table 2 suggests that Eurasia is a sink about twice the size of North America, on a per unit land area basis, the mean estimated uptake rates on North America and Eurasia are broadly similar at -32 and $-39 \text{ g C m}^{-2} \text{ yr}^{-1}$ respectively in the early 1990s (note that global uptake was high in this period relative to the rest of the decade, Fig. 2). On a vegetated area basis²³—that is, after excluding ‘bare’ areas such as deserts and ice—estimated uptake is still similar for both continents. Major climate differences between the two regions can be normalized by weighting the areas by growing season length, thereby providing an integrative index of ecosystem activity (Table 2): this again gives similar rates of uptake (per growing season day times area) on each continent. Therefore uptake rates based on mean estimates from the inversions in Table 2

are not inconsistent with expectations based on total area or bioclimatically weighted area on the two continents. New inverse modelling intercomparisons²¹ and ground-based studies⁸ are consistent with the breakdown presented here. Given the extreme uncertainty in partitioning of fluxes (Table 2), the partitioning cannot yet be regarded as definitive.

In the tropics, atmospheric inverse model calculations do not detect the large CO_2 source that would be expected from deforestation alone, but show variable results clustering around zero. This seems to imply the existence of a sink that balances the deforestation source^{12,13}, although results are poorly constrained by the sparse measurements in the tropics. If the deforestation source is $+1.6 \text{ Gt C yr}^{-1}$ for the first half of the 1990s²⁴, then a net sink of $-0.4 \text{ Gt C yr}^{-1}$ (Table 2) implies an uptake of $-2.0 \text{ Gt C yr}^{-1}$ by tropical ecosystems. Local studies show carbon uptake in a range of mature tropical forest types^{25,26}, but it is not possible to extrapolate these to the entire tropical region due to high heterogeneity of tropical ecosystems. Because of sparse atmospheric and ecological

Table 2 Estimated distribution of net land–atmosphere carbon fluxes between North America and Eurasia

	Net land–atmosphere flux, NBPII (Gt C yr ⁻¹)	Percentage of Northern Hemisphere uptake	Total land area* (10 ¹² m ²)	Net flux per unit area (g C m ⁻² yr ⁻¹)	Vegetated area† (10 ¹² m ²)	Net flux per unit vegetated area (g C m ⁻² yr ⁻¹)	Growing-season-weighted (GSW) area‡ (10 ¹⁵ m ² d)	Net flux per unit GSW area (g C m ⁻² d ⁻¹)	Modelled NPP§ (Gt C yr ⁻¹)	Net flux (~NBP) per unit NPP
North America	-0.8 (-2.1 to +0.1)	0 to 88%	25	-32	20	-40	3.1	-0.26	5 to 9	9 to 16%
Eurasia	-1.7 (-2.5 to -0.2)	13 to 100%	42	-39	36	-46	5.2	-0.33	8 to 15	11 to 21%
Northern extratropical total	-2.4 (-4.3 to -1.5)	NA	67	-36	56	-44	8.2	-0.30	13 to 23	11 to 18%
Tropical and southern temperate total	-0.4 (-1.2 to +0.8)	NA	70	-5¶	47	-8¶	15.6	-0.03¶	28 to 45	~1%¶
Global total	-2.8 (-4.3 to -1.7)	NA	137	-20	104	-27	23.8	-0.12	42 to 68	4 to 6%

A negative sign denotes a flux from the atmosphere into ecosystems. Data here are for 1990–94 from an ensemble of inverse experiments¹². The net land–atmosphere flux is the balance of terrestrial biospheric sources and sinks. Inverse modelling techniques attempt to resolve sources and sinks of carbon by back-calculating from measurements of atmospheric CO_2 . In this experiment¹², three atmospheric transport models were used, with three levels of spatial resolution (7, 12 and 17 land and ocean regions) and three temporal averaging approaches (annual average data with annual fluxes, monthly data with annual fluxes, and monthly data with monthly fluxes). Values shown are mean annual fluxes and the full range of model results in parentheses. The ranges indicate the high sensitivity of the analyses to the techniques used. The estimates are during a time period 1990–94 when the global mean land uptake was roughly 30% higher than the long-term mean (Fig. 2), thus the sinks estimated are high compared with the decadal average in Table 1, but the relative distribution between the northern continents should be roughly independent of time period. Additionally, fluxes calculated in this analysis have not been adjusted to account for river transport which will show up as a larger land sink. The tropics are shown here for comparison, but results are more uncertain due to the sparsity of the atmospheric measurement network. NA, not applicable.

* The land area relates to the regions covered in the inverse modelling analyses¹² and excludes Greenland.

† The vegetated area is estimated from a satellite-based land cover classification²³ in coincidence with the inverse model regions, and excluding land classified as ‘bare’ (that is, deserts and ice).

‡ Long-term average growing season length — calculated from the satellite normalized difference vegetation index (NDVI) from the NOAA AVHRR instrument — is the period (days) when the NDVI is above a threshold value (0.3). While the NDVI signal comes from the plant canopy, the factors that control plant growing season length also affect soil processes. The growing season length was computed for each cell in the NDVI data set, multiplied by cell area and the products summed to produce a growing season weighted area.

§ The modelled NPP values are estimates of long-term average NPP and are the highest and lowest estimates from five ecosystem models SLAVE⁴², CASA, GLO-PEM, Biome-BGC, and TEM⁴⁷.

¶ As inverse atmospheric methods detect the net effect on the atmosphere of all sources, sinks and removals they can be considered to approximate net biome productivity (NBP) over land (NBP is NPP minus losses due to death and decomposition, fire, and removals/lateral transfers).

¶¶ The tropical flux is influenced by the large deforestation emissions, leading to a lower net flux per unit land area and NBP to NPP ratio than in northern extratropical regions.

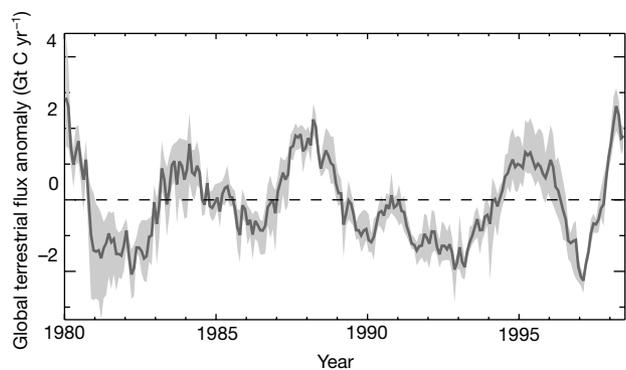


Figure 2 An illustrative plot of the interannual variability of global terrestrial carbon exchange, as deduced using inverse modelling¹⁰. The anomalies plotted on the y-axis are deviations from the long-term mean flux. The black line is the average of eight sensitivity inversions using the same model, and shaded areas represent the range of values from the inversions. Positive numbers are fluxes to the atmosphere. Although this analysis is from a single model, other analyses produce a similar pattern, although with variation in the details of the magnitude and phasing of the fluxes²⁹. Most current analyses suggest that the land biosphere plays a larger role than the oceans in the global interannual variability of atmospheric CO₂ (refs 3, 10, 29).

sampling, and complex meteorology, estimates of tropical fluxes have high uncertainty.

Interannual variability

The year-to-year variability of the average annual growth in atmospheric CO₂ concentrations is high^{27,28}. Top-down atmospheric calculations, eddy covariance flux observations, long-term ecosystem carbon budgeting studies and modelling all indicate large year-to-year variability in terrestrial metabolism^{10,17,29–36} (Fig. 2). Long-term processes, such as increasing CO₂ concentration and land-use changes, are the main drivers of the mean fluxes, but probably have a small effect on year-to-year variations³⁷. These terrestrial flux variations are probably caused by the effect of climate on carbon pools with short lifetimes (foliage, plant litter, soil microbes) through variations in photosynthesis, respiration, nutrient cycling and fire.

The net terrestrial sink appears to have increased on average from the 1980s to the 1990s (Table 1). The contribution of different processes remains difficult to quantify, but the unusually large sink in the early 1990s is thought to be largely a consequence of climate variability rather than a response to a systematic trend. Globally, there appears to be a net release of carbon to the atmosphere during warm and dry years, and a net uptake during cooler years^{30,38}. Recently, evidence for links between the El Niño/Southern Oscillation cycle and atmospheric CO₂ have become stronger^{29,30,39}.

Controls over terrestrial carbon exchange

The similarity of fluxes of carbon in North America and Eurasia per unit land area or bioclimatic index does not suggest an asymmetry between uptake processes on the two continents, in contrast to factors that may indicate spatial variability of processes. For example, nitrogen deposition is 2 to 4 times higher in Europe compared to the United States⁴⁰, and land management practices and history differ. In the United States, studies indicate that much (possibly most) of the sink is due to changing land use (including abandonment of surplus agricultural land) and more subtle management effects, such as reduced fire frequency leading to woody encroachment^{15–17,41,42}. European studies show large effects of both land use/management changes and increased tree growth

possibly due to CO₂ fertilization and N deposition^{6,17,43–45}. Chinese inventory studies also show a significant carbon sink resulting from afforestation and reforestation programs⁴⁶.

Combining the atmospherically derived fluxes presented in Table 2 (approximately equivalent to net biome productivity, NBP) with model-derived long-term averages of net primary productivity (NPP)^{43,47} suggests that 10–20% of carbon annually fixed by plants in the northern extratropics in the early 1990s remained in the biosphere (Table 2). This can be compared to inventory-based estimates of NPP to NBP ratios over large regions: for example, Nilsson *et al.*⁴⁸ estimated this ratio in Russia to be 5% in forests, 10% in wetlands and 16% in grass/shrublands, while Schulze *et al.*⁴⁹ estimate it as nearly 25% in managed European forests. All of these estimates suggest carbon accumulation in ecosystems recovering from disturbance or undergoing intensive management and, as such, are high compared with chronosequence studies that suggest much lower long-term values in natural landscapes⁵⁰.

In some regions, long-term climate changes—such as enhanced growing season in high northern latitudes and increased drought in the tropics—may be causing trends in terrestrial ecosystem processes^{17,51,52}. Much of Siberia has been warming at ~0.5 °C per decade during 1960–2000, and increased water stress has been documented in Alaska^{53,54}. Recent increases in wildfire and insects appear to have converted Siberian and North American boreal forests into carbon sources^{48,54,55}, although the northern extratropical regions as a whole are a sink. The magnitude and contribution of different processes to tropical sinks remain largely unknown, although modelling studies suggest that there may be a significant component due to increasing atmospheric CO₂ concentrations¹⁷.

Sinks of today's magnitude cannot be counted on to operate steadily into the future, as all of the key processes are likely to diminish. Uptake due to land-use change such as forest growth on agricultural land will eventually decline as the forests reach maturity. Fertilization by both CO₂ and N is expected to saturate at high levels, and as other resources become limiting⁵⁶. The effects of climate change on ecosystems is expected to reduce sinks at a global scale^{17,52}. The net terrestrial sink may thus disappear altogether in the future, although model projections of these dynamics differ greatly^{4,47,52}.

Central issues for future research

The response of ecosystems to regionally heterogeneous stimuli such as historical land use, nitrogen deposition rate, or rainfall and temperature anomalies and their effects on carbon fluxes are not predictable from global averages. Documenting these fluxes and elucidating the processes controlling them will require both regional observing systems and improved historical data on management and natural disturbances (fire, insects, and so on). Spatially extensive observations that are temporally repeatable—either inventories or a combination of inventory and eddy covariance data—are required. Uncertainty in regional and global fluxes could be reduced by improving the distribution of atmospheric CO₂ measurements over the continents and tropics: this could be done by enhancing the existing atmospheric flask sampling networks²⁸ and by using aircraft or tall towers for sampling. In addition, increased precision in measuring CO₂ concentrations from satellites, when it becomes feasible, could provide globally comprehensive observations.

Emissions from land-use changes account for a large (approximately 20%) but uncertain fraction of anthropogenic CO₂ emissions⁴. The lack of a clear atmospheric signal of tropical deforestation, and the implied large tropical sink, causes a major uncertainty in our ability to balance the terrestrial carbon cycle. The current lack of adequate data on land-use change and ecosystem processes for the tropics makes it impossible to evaluate ground-based versus atmospheric estimates as is done for the northern extratropics.

Atmospheric inverse calculations simultaneously derive ocean and land fluxes, and so uncertainty in terrestrial and marine fluxes are not independent. Understanding and stabilization of the Earth system will require these uncertainties to be addressed by efforts linking terrestrial ecology with the other Earth sciences. □

1. Bender, M., Ellis, T., Tans, P., Francey, R. & Lowe, D. Variability in the O₂/N₂ ratio of southern hemisphere air, 1991–1994: Implications for the carbon cycle. *Glob. Biogeochem. Cycles* **10**, 9–21 (1996).
2. Keeling, R. F., Piper, S. C. & Heimann, M. Global and hemispheric CO₂ sinks deduced from changes in atmospheric O₂ concentration. *Nature* **381**, 218–221 (1996).
3. Rayner, P. J., Enting, I. G., Francey, R. J. & Langenfelds, R. Reconstructing the recent carbon cycle from atmospheric CO₂, δ¹³C and O₂/N₂ observations. *Tellus B* **51**, 213–232 (1999).
4. Prentice, I. C. *et al.* in *Climate Change 2001: The Scientific Basis* (eds Houghton, J. T. & Yihui, D.) Ch. 3, 183–237 (Cambridge Univ. Press, Cambridge, 2001).
5. Brown, S. in *Climate Change 1995—Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses* (eds Watson, R. T., Zinyowera, M. C., Moss, R. H. & Dokken, D. J.) 773–797 (Cambridge Univ. Press, Cambridge, 1996).
6. Spiecker, H., Mielikäinen, K., Köhl, M. & Skovsgaard, J. P. *Growth Trends in European Forests* (Springer, Berlin, 1996).
7. Brown, S. L. & Schroeder, P. E. Spatial patterns of aboveground production and mortality of woody biomass for eastern US forests. *Ecol. Appl.* **9**, 968–980 (1999).
8. Pacala, S. W. *et al.* Consistent land- and atmosphere-based US carbon sink estimates. *Science* **292**, 2316–2320 (2001).
9. Tans, P. P., Fung, I. Y. & Takahashi, T. Observational constraints on the global atmospheric CO₂ budget. *Science* **247**, 1431–1438 (1990).
10. Bousquet, P. *et al.* Regional changes in carbon dioxide fluxes of land and oceans since 1980. *Science* **290**, 1342–1346 (2000).
11. Baker, D. *Sources and Sinks of Atmospheric CO₂ Estimated from Batch Least-Squares Inversions of CO₂ Concentration Measurements*. Thesis, Princeton Univ. (2000).
12. Peylin, P., Baker, D., Sarmiento, J., Ciais, P. & Bousquet, P. Influence of transport uncertainty on annual mean versus seasonal inversion of atmospheric CO₂ data. *J. Geophys. Res. D* (submitted).
13. Heimann, M. *Atmospheric Inversion Calculations Performed for IPCC Third Assessment Report Chapter 3 (The Carbon Cycle and Atmospheric CO₂)* (Max-Planck-Institute für Biogeochemie, Jena, 2001).
14. Ciais, P., Tans, P. P., Trolier, M., White, J. W. C. & Francey, R. J. A large northern-hemisphere terrestrial CO₂ sink indicated by the ¹³C/¹²C ratio of atmospheric CO₂. *Science* **269**, 1098–1102 (1995).
15. Houghton, R. A., Hackler, J. L. & Lawrence, K. T. The US carbon budget: Contributions from land-use change. *Science* **285**, 574–578 (1999).
16. Schimel, D. *et al.* Contribution of increasing CO₂ and climate to carbon storage by ecosystems in the United States. *Science* **287**, 2004–2006 (2000).
17. McGuire, A. D. *et al.* Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO₂, climate and land-use effects with four process-based ecosystem models. *Glob. Biogeochem. Cycles* **15**, 183–206 (2001).
18. Denning, A. S. *et al.* Three-dimensional transport and concentration of SF₆—A model intercomparison study (TransCom 2). *Tellus B* **51**, 266–297 (1999).
19. Bousquet, P., Ciais, P., Peylin, P., Ramonet, M. & Monfray, P. Inverse modeling of annual atmospheric CO₂ sources and sinks I. Method and control inversion. *J. Geophys. Res. D* **104**, 26161–26178 (1999).
20. Kaminski, T., Heimann, M. & Giering, R. A coarse grid three-dimensional global inverse model of the atmospheric transport—1. Adjoint model and Jacobian matrix. *J. Geophys. Res. D* **104**, 18535–18553 (1999).
21. Gurney, K. R., Rayner, P., Law, R. & Denning, S. Atmospheric carbon budget inversion intercomparison: preliminary results. *Trans. Am. Geophys. Union* **81**, 276 (2000).
22. Fan, S. *et al.* A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. *Science* **282**, 442–446 (1998).
23. DeFries, R. S. *et al.* Mapping the land surface for global atmosphere-biosphere models: toward continuous distributions of vegetation's functional properties. *J. Geophys. Res. D* **100**, 20867–20882 (1995).
24. Houghton, R. A. A new estimate of global sources and sinks of carbon from land-use change. *Eos* **81**, S281 (2000).
25. Malhi, Y. *et al.* Carbon dioxide transfer over a Central Amazonian rain forest. *J. Geophys. Res. D* **103**, 31593–31612 (1998).
26. Phillips, O. L. *et al.* Changes in the carbon balance of tropical forests: Evidence from long-term plots. *Science* **282**, 439–442 (1998).
27. Keeling, C. D. & Whorf, T. P. in *Trends: A Compendium of Data on Global Change* (Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee, 2001).
28. Conway, T. J., Tans, P. P., Waterman, L. S. & Thoning, K. W. Evidence for interannual variability of the carbon-cycle from the National Oceanic and Atmospheric Administration/Climate Monitoring and Diagnostics Laboratory global air-sampling network. *J. Geophys. Res. D* **99**, 22831–22855 (1994).

29. Rayner, P. J., Law, R. M. & Dargaville, R. The relationship between tropical CO₂ fluxes and the El Niño–Southern Oscillation. *Geophys. Res. Lett.* **26**, 493–496 (1999).
30. Vukicevic, T., Braswell, B. H. & Schimel, D. A diagnostic study of temperature controls on global terrestrial carbon exchange. *Tellus B* **53**, 150–170 (2001).
31. Goulden, M. L., Munger, J. W., Fan, S. M., Daube, B. C. & Wofsy, S. C. Exchange of carbon dioxide by a deciduous forest: Response to interannual climate variability. *Science* **271**, 1576–1578 (1996).
32. Kindermann, J., Würth, G., Kohlmaier, G. H. & Badeck, F. W. Interannual variation of carbon exchange fluxes in terrestrial ecosystems. *Glob. Biogeochem. Cycles* **10**, 737–755 (1996).
33. Parton, W. J. *et al.* Observations and modeling of biomass and soil organic-matter dynamics for the grassland biome worldwide. *Glob. Biogeochem. Cycles* **7**, 785–809 (1993).
34. Kelly, R. H. *et al.* Intra-annual and interannual variability of ecosystem processes in shortgrass steppe. *J. Geophys. Res. D* **105**, 20093–20100 (2000).
35. Prentice, I. C., Heimann, M. & Sitch, S. The carbon balance of the terrestrial biosphere: Ecosystem models and atmospheric observations. *Ecol. Appl.* **10**, 1553–1573 (2000).
36. Knapp, A. K. & Smith, M. D. Variation among biomes in temporal dynamics of aboveground primary production. *Science* **291**, 481–484 (2001).
37. Houghton, R. A. Interannual variability in the global carbon cycle. *J. Geophys. Res. D* **105**, 20121–20130 (2000).
38. Braswell, B. H., Schimel, D. S., Linder, E. & Moore, B. The response of global terrestrial ecosystems to interannual temperature variability. *Science* **278**, 870–872 (1997).
39. Yang, X. & Wang, M. X. Monsoon ecosystems control on atmospheric CO₂ interannual variability: inferred from a significant positive correlation between year-to-year changes in land precipitation and atmospheric CO₂ growth rate. *Geophys. Res. Lett.* **27**, 1671–1674 (2000).
40. Holland, E. A., Dentener, F. J., Braswell, B. H. & Sulzman, J. M. Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry* **46**, 7–43 (1999).
41. Archer, S., Boutton, T. W. & Hibbard, K. A. in *Global Biogeochemical Cycles and Their Interrelationship with Climate* (eds Schulze, E. D.) 115–137 (Academic, London, 2001).
42. Casperson, J. *et al.* Carbon accumulation in U.S. forests is caused overwhelmingly by changes in land use rather than CO₂ or N fertilization or climate change. *Science* **290**, 1148–1151 (2001).
43. Friedlingstein, P. *et al.* On the contribution of the biospheric CO₂ fertilization to the missing sink. *Glob. Biogeochem. Cycles* **9**, 541–556 (1995).
44. Kauppi, P. E., Mielikäinen, K. & Kuusela, K. Biomass and carbon budget of European forests, 1971 to 1990. *Science* **256**, 70–74 (1992).
45. Valentini, R. *et al.* *Accounting for Carbon Sinks in the Biosphere, European Perspective* (CARBOEUROPE European Office, Jena, 2000).
46. Fang, J. Y., Chen, A. P., Peng, C. H., Zhao, S. Q. & Ci, L. Changes in forest biomass carbon storage in China between 1949 and 1998. *Science* **292**, 2320–2322 (2001).
47. Cramer, W. *et al.* Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Glob. Change Biol.* **5**, 1–15 (1999).
48. Nilsson, S. *et al.* *Full Carbon Account for Russia* (International Institute for Applied Systems Analysis, Laxenburg, 2000).
49. Schulze, E. D. *et al.* in *Carbon and Nitrogen Cycling in European Forest Ecosystems* (ed. Schulze, E. D.) 468–491 (Springer, Berlin, 2000).
50. Harden, J. W., Sundquist, E. T., Stallard, R. F. & Mark, R. K. Dynamics of soil carbon during deglaciation of the Laurentide ice-sheet. *Science* **258**, 1921–1924 (1992).
51. Keyser, A. R., Kimball, J. S., Nemani, R. R. & Running, S. W. Simulating the effects of climate change on the carbon balance of North American high-latitude forests. *Glob. Change Biol.* **6**, 185–195 (2000).
52. Cramer, W. *et al.* Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Glob. Change Biol.* **7**, 357–373 (2001).
53. Jones, P. D., New, M., Parker, D. E., Martin, S. & Rigor, I. G. Surface air temperature and its changes over the past 150 years. *Rev. Geophys.* **37**, 173–199 (1999).
54. Barber, V. A., Juday, G. P. & Finney, B. P. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* **405**, 668–673 (2000).
55. Kurz, W. A. & Apps, M. J. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecol. Appl.* **9**, 526–547 (1999).
56. Field, C. B., Chapin, F. S., Matson, P. A. & Mooney, H. A. Responses of terrestrial ecosystems to the changing atmosphere—a resource-based approach. *Annu. Rev. Ecol. Syst.* **23**, 201–235 (1992).

Acknowledgements

This Progress Article arose from the International Workshop on Integrated Carbon Research and Observations, held on 16–20 October 2000. This workshop was organized under the auspices of the International Geosphere–Biosphere Programme (IGBP) and the Global Terrestrial Observing System (GTOS), and was co-funded by NOAA, the NSF, NASA, the US Department of Energy, the US Department of Interior/US Geological Survey, the US Department of Agriculture and the International Geosphere Biosphere Programme. D.S.S. was also supported by the European Commission, NASA, and the Bundesministerium für Bildung und Forschung.

Correspondence and requests for materials should be addressed to D.S.S. (email: schimel@ucar.edu).