Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems

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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 CO_2 and O_2 (as O_2:N_2 ratios) make it possible to partition the uptake of atmospheric CO_2 between the land and ocean with increased confidence[1–3]. Global carbon budgets have been updated in the most recent IPCC assessment[4] using this approach (Table 1). The net terrestrial biospheric flux between the land and atmosphere was about −0.2 gigatonnes of carbon per year ($\mathrm{Gt\,C\,yr^{-1}}$) in the 1980s and $-1.4\,\mathrm{Gt\,C\,yr^{-1}}$ 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 $+2.5\,\mathrm{Gt\,C\,yr^{-1}}$ for the 1980s, largely from deforestation in the tropics[4]. 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 $-4\,\mathrm{Gt\,C\,yr^{-1}}$.

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 CO_2: this evidence has been obtained from analysis of land inventory data[5–8], atmospheric CO_2 data[9–13], atmospheric O_2 data[1–3], isotopic analyses[3,14], studies of land-use change[15] 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 CO_2 from the distribution of atmospheric concentrations, resulting in a range of estimates of the northern extratropical net land sink from −0.6 to $-2.3\,\mathrm{Gt\,C\,yr^{-1}}$ in the 1980s[13].

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 used[12], 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 America and Eurasia[3,11,12,19–21], in contrast to earlier reports of a dominant sink in North America[22]. Given the controversy over the

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

	1980s* ($\mathrm{Gt\,C\,yr^{-1}}$)	1990s* ($\mathrm{Gt\,C\,yr^{-1}}$)
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).

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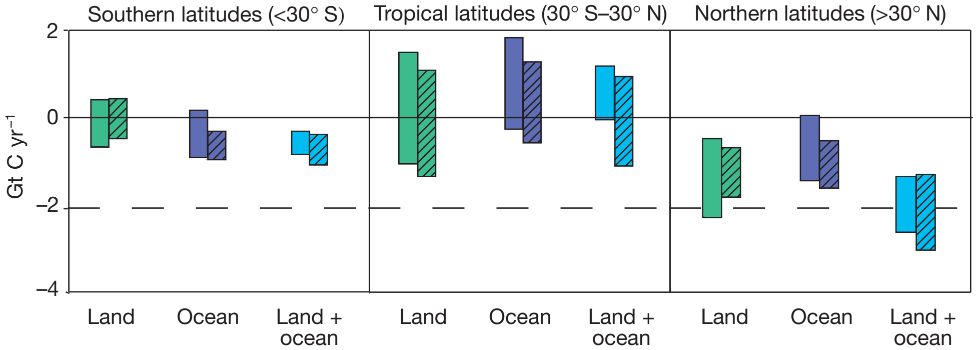

Figure 1 Zonal distribution of terrestrial and oceanic carbon fluxes. These data were deduced from eight inverse models using different techniques and sets of atmospheric observations after accounting for fossil-fuel emissions (not shown)[13]. Results are shown for the 1980s (plain bars) and for 1990–96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

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 $-39\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ 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 basis[23]—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 intercomparisons[21] and ground-based studies[8] 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 $+1.6\,\mathrm{Gt\,C\,yr^{-1}}$ for the first half of the 1990s[24], then a net sink of $-0.4\,\mathrm{Gt\,C\,yr^{-1}}$ (Table 2) implies an uptake of $-2.0\,\mathrm{Gt\,C\,yr^{-1}}$ 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 sampling, and complex meteorology, estimates of tropical fluxes have high uncertainty.

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

	Net land–atmosphere flux, NBP‖ (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} y^{-1})	Vegetated area† (10^{12} m^2)	Net flux per unit vegetated area (g C m^{-2} y^{-1})	Growing-season-weighted (GSW) area‡ (10^{15} m^2 d)	Net flux per unit GSW area (g C m^{-2} d^{-1})	Modeled 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 experiments[12]. 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 experiment[12], 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 analyses[12] and excludes Greenland.

† The vegetated area is estimated from a satellite-based land cover classification[23] 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 SLAVE[42], CASA, GLO-PEM, Biome-BGC, and TEM[47].

‖ 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.

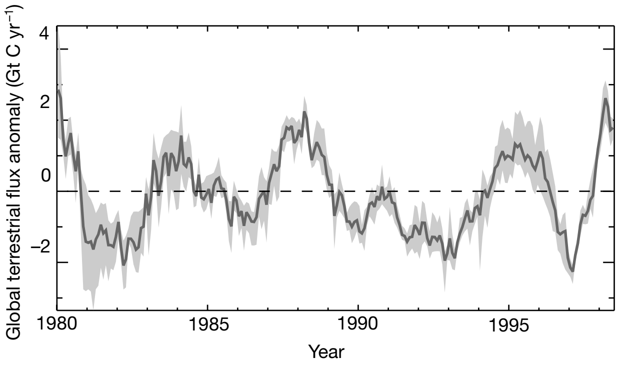

Figure 2 An illustrative plot of the interannual variability of global terrestrial carbon exchange, as deduced using inverse modelling[10]. The anomalies plotted on the *y* axis are deviations from the long-term mean flux. The black line is the average of eight sensitivity inversions using the same model, 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 fluxes[29]. Most current analyses suggest that the land biosphere plays a larger role than the oceans in the global interannual variability of atmospheric CO_2 (refs 3, 10, 29).

Interannual variability

The year-to-year variability of the average annual growth in atmospheric CO_2 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 CO_2 concentration and land-use changes, are the main drivers of the mean fluxes, but probably have a small effect on year-to-year variations[37]. 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 CO_2 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 States[40], 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 CO_2 fertilization and N deposition[6,17,43–45]. Chinese inventory studies also show a significant carbon sink resulting from afforestation and reforestation programs[46].

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 landscapes[50].

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 CO_2 concentrations[17].

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 CO_2 and N is expected to saturate at high levels, and as other resources become limiting[56]. 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 CO_2 measurements over the continents and tropics: this could be done by enhancing the existing atmospheric flask sampling networks[28] and by using aircraft or tall towers for sampling. In addition, increased precision in measuring CO_2 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 CO_2 emissions[4]. 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. □

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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.

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