



Lowland rainforest, Borneo (F Lanting) © Minden Pictures/FLPA

Terrestrial carbon sinks – uncertain explanations

R A Houghton

Woods Hole Research Center, USA

The carbon cycle is fundamental to life on Earth and it determines the amount of carbon

Carbon is the basis of life on Earth. It is incorporated into plants through photosynthesis, absorbed by animals through their food, present in the atmosphere as carbon dioxide, locked into rock as limestone, and pressed into fossil fuels such as coal and oil. In the Jurassic age, there was much more carbon in the atmosphere than there is now. The carbon taken up by plants on land and in the sea gradually, over millennia, exceeded the amount released during decay, and this 'excess' carbon became locked away as fossil fuels beneath the surface of the planet. In effect, life on Earth was acting as a 'carbon sink'. For the last two centuries, this trend has been drastically reversed as forests have been reduced and fossil fuels have been burnt, meaning that more carbon has been released into the atmosphere than has been absorbed. There is considerable concern that this is leading directly to global warming. 'Carbon sinks' are now the focus of considerable study.

Although the oceans are currently the greatest carbon sink, terrestrial carbon sinks are also important. The greatest terrestrial carbon sinks occur in young, growing forests, because a hectare of trees holds up to 50 times more carbon than a hectare of grasses or crops. Older forests and soils may also accumulate carbon but the rates are generally low compared with the rate for young trees. Nevertheless, low rates over large areas, including grasslands as well as forests, can yield a sink that is globally large. Because the

amount of carbon in soils is large and variable, it is difficult to measure an annual carbon sink, even in a small, well-defined area. To measure a change globally is nearly impossible. Given that terrestrial ecosystems are accumulating carbon in some regions and releasing it in others, it is very difficult to determine, directly, the magnitude of the terrestrial carbon sink. (See Box 1 for a description of the methods used to measure or infer the magnitude of terrestrial sinks.)

Direct measurement of changes in the concentrations of carbon dioxide and oxygen in the atmosphere provides one estimate of the global terrestrial sink (Table 1). Nearly half of the carbon released each year from fossil fuel combustion accumulates in the atmosphere. The oceans and some terrestrial ecosystems take up the rest. According to a recent global analysis based on changes in the concentrations of carbon dioxide and oxygen (Plattner *et al.*, in review), the world's terrestrial ecosystems (vegetation and soils) were a small net sink during the 1980s and 1990s.

Independent of these estimates of a net terrestrial sink, changes in land use (including deforestation – whether for settlements or agriculture – reforestation, and the management of forests and wood products) are calculated to have released an average of 2.0×10^{15} grams of carbon per year (PgC yr^{-1}), and slightly more during the 1990s (Houghton, in press). These estimates include the releases of carbon from the oxidation of wood products and logging debris, as well as

Box 1. Methods that are used to measure or infer carbon sinks

1. Global budgets based on atmospheric data and models
The CO₂ concentration of air is measured weekly at a network of nearly 100 sites around the world. Using models of atmospheric transport, scientists calculate the surface sources and sinks of carbon that explain the observed variation in CO₂ concentrations. This inverse modelling approach can also be used to distinguish terrestrial vs. oceanic carbon sinks when the atmospheric measurements include temporal variations in O₂ and in the isotopic composition of CO₂ (i.e., ¹³CO₂; Table 5).

2. Global budgets based on models of oceanic carbon uptake

Models of the oceans' carbon cycle (including carbon chemistry and oceanic circulation) can be used with temporal patterns of atmospheric CO₂ and fossil fuel emissions to infer the net terrestrial sources and sinks of carbon. This approach yields a global value (no regional distinctions), but can be applied over the last two centuries. CO₂ concentrations before 1957, when direct measurements began, are obtained from analysis of the air trapped in bubbles in Greenland and Antarctic glaciers.

3. Regional carbon budgets constructed from forest inventories

Most of the developed nations have national forest inventories that monitor the volume of wood in forests. Changes in volumes over time indicate sources or sinks of carbon. Supplementary information can be used to infer associated changes in woody debris, wood products, and soil carbon – those components that are not directly measured in the inventories.

4. Stand-level direct measurement of CO₂ flux (from towers)

Direct measurement of CO₂ flux over an ecosystem is obtained by linking CO₂ concentrations in air with the upward or downward movement of that air (the eddy covariance technique). The approach yields hourly estimates of flux for

areas of a few km², but is difficult to scale up to larger regions. Because net fluxes of carbon are generally small relative to the gross daytime and night time fluxes, the approach is better suited for determining short-term responses of photosynthesis and respiration to variations in temperature and moisture than to determining annual carbon budgets.

5. Physiologically-based process models of ecosystems
Ecosystem- and global-scale models simulate changes in carbon storage as a result of environmentally induced changes in photosynthesis, respiration, growth, litter fall and decomposition. The advantage of such process-based models is that they can be used to distinguish the effects of different factors on carbon storage. The disadvantage is that it is difficult to know whether they include all of the important processes.

6. Carbon models based on changes in land use

These models are based on the changes in vegetation and soil that accompany a change in land use. When forests are converted to agricultural land, for example, the amount of carbon in the vegetation and soil is reduced. When open lands are afforested, carbon stocks increase. The rates of loss and increase vary with land use and type of ecosystem, but they are documented for many systems. Most of the error in the calculated flux of carbon results from uncertainties in rate of deforestation and wood harvest.

Estimates of carbon flux based on changes in land use can theoretically identify sources and sinks resulting from direct human activity, but to do so requires baseline information on the rates of forest growth that would have existed in the absence of changes in CO₂, N, climate, or other environmental variables. Such data are generally unavailable. Nevertheless, the method, in combination with methods that measure a net source or sink (methods 1–4 above), has the potential to distinguish sinks resulting from direct

the accumulations of carbon in regrowing forests. Strangely, the difference between the net terrestrial sink and the emissions from land-use change suggests that there is a residual terrestrial sink, not well understood, that locked away as much as 3.0 PgC yr⁻¹ during the last two decades (Table 1).

The exact magnitude, location and cause of this residual terrestrial sink are uncertain, but it is important to understand the mechanisms responsible for at least two reasons. First, the Kyoto Protocol requires that sinks resulting directly from human activity (e.g., planting trees) be distinguished from sinks unrelated to direct human management (e.g., growth enhancement through CO₂ fertilisation), so as to avoid 'undue credits'. Second, some potential mechanisms are more likely to persist into the future than others are. Without a greater understanding of the global carbon cycle, plans for remedial action will be, at best, reliant on some guesswork. There is even the chance of inadvertently worsening the situation by harming existing sinks.

The mechanisms proposed as being responsible for terrestrial sinks fall into two broad categories (Table 2):

- Physiological or metabolic factors that affect rates of photosynthesis, respiration, growth, and decay. These factors include elevated concentrations of atmospheric CO₂, increased availability of nutrients, and changes in temperature and rainfall, any of which could increase growth rates in forests – locking more carbon away from

the atmosphere. These factors generally result indirectly from human activities.

- Disturbance and recovery mechanisms, including both natural disturbances and the direct effects of changes in land use and management. Disturbances affect the mortality of forest stands and thus the age structure of forests; recovering forests are sinks for carbon. Different land management strategies may also affect the amount of carbon stored in non-forest ecosystems.

Physiological or metabolic mechanisms responsible for the current sink

The longest-standing physiological mechanism proposed for the accumulation of carbon on land is CO₂ fertilisation. Horticulturalists have long known that annual plants respond to higher levels of CO₂ with increased rates of growth. The concentration of CO₂ in greenhouses is often deliberately increased to make use of this effect. Similarly, experiments have shown that most C₃ plants (all trees, most crops, and vegetation from cold regions) respond to elevated concentrations of CO₂ with increased rates of photosynthesis and growth.

Despite the observed stimulatory effects of CO₂ on photosynthesis and plant growth, it is not clear that the effects will result in an accumulation of carbon (that is, a net sink) in

Table 1. The global carbon budget. Units are PgC yr⁻¹

Negative values refer to withdrawals of carbon from the atmosphere; that is, sinks.

	1980s	1990s
Fossil fuel emissions*	5.4 ± 0.3	6.3 ± 0.4
Atmospheric increase*	3.3 ± 0.1	3.2 ± 0.2
Oceanic uptake**	-1.7 ± 0.6	-2.4 ± 0.7
Net terrestrial flux**	-0.4 ± 0.7	-0.7 ± 0.8
Land-use change***	2.0 ± 0.8	2.2 ± 0.8
Residual 'terrestrial' flux	-2.4 ± 1.1	-2.9 ± 1.1

* Prentice *et al.* (2001)

Table 2. Proposed mechanisms for carbon sinks*

Physiological or metabolic mechanisms (often an indirect effect of human activities)

- n CO₂ fertilisation
- n N fertilisation
- n Tropospheric ozone, acid deposition
- n Changes in climate (temperature, moisture, length of growing season, cloudiness)

Disturbance and recovery mechanisms

Direct effects of human activities

- l Large-scale regrowth of forests following human disturbance (includes recovery from logging and agricultural abandonment)
- l Fire suppression and woody encroachment
- l Decreased deforestation
- l Improved agricultural practices
- l Wood products and landfills

Natural disturbances

- n Erosion and re-deposition of sediment
- n Large-scale regrowth of forests following natural disturbance

* Some of these mechanisms enhance growth; some reduce the decomposition. In some cases these same mechanisms may also yield releases of carbon to the atmosphere.

l Mechanisms nominally included in analyses of land-use change

either plants or soils. Annual plants and most crops do not accumulate carbon for more than a year. Furthermore, the stimulatory effects of CO₂ have generally been observed in short-term experiments, while over longer intervals the effects are often reduced or absent. For example, plants often acclimate to higher concentrations of CO₂ so that their rates of photosynthesis and growth return to the rates observed before the concentration was raised (Oren *et al.*, 2001). The few studies conducted at higher levels of integration or complexity, such as mature trees or whole ecosystems, including soils as well as vegetation, suggest much reduced responses (Table 3). The trend suggests that, as the level of complexity or the number of interacting processes increases, the effects of CO₂ fertilisation are diminished.

Even an increase in growth need not lead to an increase in carbon storage. If the increased growth is largely labile (easily decomposed), then it may be decomposed rapidly with little change in carbon storage. Recent results from a loblolly pine forest in North Carolina support this minimum change. Elevated CO₂ increased litter production (with a turnover time of about three years) but did not increase carbon accumulation in deeper layers of the soil (Schlesinger and Lichter,

2001).

Nitrogen fertilisation is another mechanism proposed to increase the amount of carbon stored on land. Human activity has increased the abundance of biologically active forms of nitrogen (NO_x and NH₄), largely through the production of fertilisers, the planting of legumes, and the combustion of fossil fuels. Because the availability of N is thought to limit plant growth in temperate-zone ecosystems, the addition of N is expected to increase growth and, perhaps, carbon storage. Adding N to forests has been shown to increase growth and may increase the residence time of soil organic matter, but added N is also immobilised in soils and lost from the ecosystem, becoming largely unavailable in either case. In whole-ecosystem experiments, additions of isotopically-labelled N showed that much of the label appeared in soil rather than in plant biomass, suggesting that nitrogen deposition was unlikely to be a major contributor to a terrestrial carbon sink in northern forests. Furthermore, above some undetermined level, additional N may saturate ecosystems, leading to reduced productivity and, perhaps, reduced amounts of carbon.

Atmospheric pollutants, such as tropospheric ozone, and sulphur and nitrogen in acid rain, may have negative effects on growth, perhaps reducing carbon sinks. Experimental studies show leaf injury and reduced growth in crops and trees exposed to ozone, and reduced forest growth in North America and Europe is associated with elevated levels of ozone. Acidification of soil as a result of deposition of NO₃⁻ and SO₄²⁻ in precipitation depletes the soils of essential plant nutrients and increases the mobility and toxicity of aluminium. Although atmospheric pollution generally reduces growth, its effects on carbon storage are not known. It could potentially increase carbon storage if it reduces decomposition of organic matter more than it reduces growth.

Climatic variability and climatic change can also change the amount of carbon held on land. Year-to-year variation in temperature and precipitation, in affecting rates of photosynthesis and respiration, is thought to be the major factor responsible for large year-to-year

variation in the growth rate of atmospheric CO₂. Over the longer-term, the effects of climate change are not as clear. Satellite records of 'greenness' over boreal and temperate Europe over two decades show a lengthening of the growing season, suggesting greater growth and carbon storage. Measurements of CO₂ flux in these ecosystems, however, do not consistently show a net uptake of carbon in response to warm temperatures, presumably because warmer soils release more carbon than plants take up. Increased temperatures in the tropics may reduce carbon storage, especially if

Table 3. Increases observed for a 100% increase in CO₂ concentrations (modified from Prentice *et al.*, 2001)

60% increase in photosynthesis of young trees
33% average increase in growth rates of crops
25% increase in growth of a young pine forest
14% average increase in biomass of grasslands and crops

higher temperatures are associated with drier climates and more fires. Prediction of future terrestrial sinks resulting from climate change requires an understanding of not only plant and microbial physiology, but also the regional aspects of future climate change.

Disturbance and recovery mechanisms responsible for the current sink

Terrestrial sinks also result from the recovery (growth) of ecosystems disturbed in the past. The disturbances may be either natural (insects, disease, fires) or human-induced (management and changes in land-use) (Table 2). Changes in land use and management are an especially significant subset of disturbance and recovery mechanisms because they represent the changes in carbon resulting directly from human activity: the subset that qualifies for credits and debits in a Kyoto carbon accounting system. A recent analysis of changes in land use, including the expansion and abandonment of croplands and pastures, the harvest of wood, and the fate of wood products, calculated a global release of 2.0 PgC yr⁻¹ for the 1980s and 2.2 PgC yr⁻¹ for the 1990s (Table 1). This net release includes carbon sinks that were generally similar in temperate-zone and tropical lands (0.4 – 0.7 PgC yr⁻¹; Table 4), but the releases of carbon exceeded the sinks in the tropics and were largely offset by the sinks outside the tropics.

Repeated measurements of timber volumes in forests provide an independent measure of carbon sources and sinks in forests. A recent analysis of such data for the forests of North America, Europe, Russia and China, accounting for changes in living and dead trees, soils, and wood products, showed a sink of 0.7 PgC yr⁻¹ around 1990 (Goodale *et al.*, 2002). The estimate explains a portion of the global net terrestrial sink (Table 1), and a sink of similar magnitude might also be found in non-forest ecosystems (Houghton *et al.*, 1999; Pacala *et al.*, 2001).

The accumulation of carbon in forests, as measured by forest inventories, does not, by itself, identify the mechanisms responsible. However, a recent analysis of forest growth and mortality in five states of the US suggests that 98% of the

current accumulation of carbon in trees is explained by age structure, without requiring growth enhancement due to CO₂, N fertilisation, or other factors (Caspersen *et al.*, 2000). The finding is at odds with explanations based on physiological mechanisms.

Which mechanisms are most important?

Until recently, the most common explanations for the residual carbon sink were factors that affect the physiology of plants and microbes: CO₂ fertilisation, N deposition and climatic variability. Several recent findings have started to shift the explanation to include management practices and disturbances that affect the age structure of forests. For example, the suggestion that CO₂ fertilisation may be less important in forests than in short-term greenhouse experiments (Table 3) was supported by a recent experiment in a North American loblolly pine plantation. Investigators found that elevated concentrations of CO₂ increased the accumulation of carbon in trees during the first three years of the experiment but not in subsequent years (Oren *et al.*, 2001). On a larger scale, the finding by Caspersen *et al.* (2000; see above) suggests either that the physiological effects of CO₂, N, and climate have been unimportant in these forests, or that their effects were offset by other influences, for example a warming-enhanced increase in rates of respiration.

Analyses of land-use change suggest that recovery from past human activities (logging, fire suppression and abandonment of farms) accounts for only 10 – 30% of the observed accumulation of carbon in US trees (Houghton *et al.*, 1999). This finding is inconsistent with the 98% value calculated by Caspersen *et al.* (2000). The difference might be explained by past natural disturbances (not included in analysis of land-use change). However, fire suppression was included, and other disturbances in the US are unlikely to have been large relative to direct human management. Thus, these two studies disagree as to the relative importance of physiological vs. disturbance mechanisms in explaining the current sink.

Recovery from past disturbances also seems unlikely to explain a carbon sink in the tropics that is large enough to offset the emissions from deforestation, as global budgets based on atmospheric data and models suggest. Thus, CO₂

fertilisation or climatic trends may be more important in the tropics than at mid-latitudes. The sinks observed with CO₂ flux measurements in a limited number of undisturbed tropical forests support this conclusion, but the lack of systematic forest inventories over large areas in the tropics precludes a more definitive test of where forests are accumulating carbon and where they are losing it. Thus, the factors responsible for the residual terrestrial sink (physiology or age structure) remain uncertain.

Implications for a carbon accounting system

To stop the accumulation of carbon dioxide in the atmosphere will eventually require large reductions in carbon emissions. In the short term, however, to gain time for development of alternatives to fossil fuels, enhancing carbon sinks on land may be an effective method of slowing the rate of atmospheric carbon dioxide accumulation. However, the Kyoto Protocol allows only certain sinks are to be credited: those resulting from direct human activity since 1990. Attributing terrestrial sinks to direct (management), as opposed to indirect (environmental) or natural effects, is scientifically difficult, however. One might demonstrate mechanisms through

Table 4. Activities included in analyses of land-use change and estimates of the associated sources (+) and sinks (–) of carbon

for the 1990s) (from Houghton, in press)

Activity	Globe	Tropical Temperate and regions boreal zones	
1. Deforestation	2110*	130	2240
2. Afforestation	–100	–80	–190
3. Reforestation (agricultural abandonment) 0*	0*	–60	–60
4. Harvest/Management	190	120	310
a. Products	200	390	590
b. Slash	420	420	840
c. Regrowth	–430	–690	–1120
5. Fire suppression	0	–30	–30
6. Non-forests			
a. Agricultural soils	0	20	20
b. Woody encroachment**	–	–60	–60
Total	2200	40	2240

* Only the net effect of shifting cultivation is included. The gross fluxes from repeated clearing of fallow lands and temporary abandonment are not included.

** Probably an underestimate. The estimate is for the US only, and

Table 5. Characteristics of methods used to estimate terrestrial sinks

	Geographic limitations	Temporal resolution	Attribution of mechanism(s)	Precision
Inverse modelling: atmospheric data	Poor in tropics	Monthly to annual	No	Low
Inverse modelling: oceanic data	No geographic resolution	Annual	No	Low
Forest inventories able	Nearly non-existent in the tropics	5 – 10 years	Yes (age classes)	High for biomass; variable for soil carbon
CO ₂ flux	Site specific (a few km ²); difficult to scale up	Hourly to annual	No	Some problems with windless conditions
Physiologically-based models	None	Hourly to annual	Yes	Variable; difficult to validate
Land-use models	Data limitations in	Annual	Yes	Low

controlled experiments, but experiments distinguishing the causative factors of forest growth would be difficult to set up and interpret. Data from forest inventories may reveal whether rates of growth have been enhanced (Caspersen *et al.*, 2000), but additional information is required. In the absence of enhanced growth, for example, recovering forests must be shown to have resulted from past human management, as opposed to past natural disturbances. And, if growth rates have been enhanced, other data must be used to distinguish whether enhancement is the result of environmental factors (for example, N deposition) or management (for example, N application).

The most straightforward approach for evaluating the direct effects of management is to multiply the per hectare changes in vegetation and soil that follow a change in land use by the areas annually cleared, abandoned, or harvested. Bookkeeping models that include the delayed effects of decay and regrowth have been developed for this calculation (Houghton *et al.*, 1999). Indirect effects and natural disturbances are excluded from the analyses, and thus, by definition, the analyses evaluate the direct effects of human activities. In contrast, most methods that measure changes in terrestrial carbon stocks do not distinguish among mechanisms (see Box 1).

Implications for the future

Accurate prediction of the future behaviour of terrestrial sinks, and thus their effects on future concentrations of atmospheric CO₂, is reliant upon improving our understanding of carbon sink mechanisms. Physiological considerations suggest that the photosynthetic response to increased CO₂ concentrations will continue to increase as concentrations rise. At very high concentrations, the response will saturate, but considerable carbon will have accumulated on land before concentrations reach these levels.

In contrast to models based on physiology only, models that include land-use change and management suggest that the current terrestrial sink is likely to decrease much sooner. It might even become a net release in the future. One analysis suggests that the current sink in the US will decline from a current value of 0.5 PgC yr⁻¹ to 0.21 PgC yr⁻¹ by 2050 and to 0.13 PgC yr⁻¹ by 2100, as growing forests

mature and come to a new level of biomass that is in equilibrium with harvests (Hurt *et al.*, 2002).

In conclusion, various ecological mechanisms (*e.g.*, CO₂ fertilisation, N deposition, climatic variability) have been shown experimentally to have short-term effects on physiological processes controlling the amount of carbon in terrestrial ecosystems. However, it is unclear which of these mechanisms has been important in the past 10 – 100 years, and which will be most important in the future. A major portion of the sink in the northern mid-latitudes (although perhaps not in the tropics) is a result of recovery from past changes in land use and land management. To the extent that these direct human actions explain most of the current (and future) sink, attribution and thus accounting become more tractable, but the continued functioning of the sink is limited and largely dependent on deliberate actions (*e.g.*, afforestation, sustainable forest management, preservation).

References

- Caspersen J P, Pacala S W, Jenkins J C, Hurt G C *et al.* (2000) Contributions of land-use history to carbon accumulation in U.S. forests. *Science*, **290**, 1148 – 1151.
- Goodale C L, Apps M J, Birdsey R A, Field C B *et al.* (2002) Forest carbon sinks in the northern hemisphere. *Ecological Applications*, **12**, 891 – 899.
- Houghton R A (in press) Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use 1850 – 2000. *Tellus*.
- Houghton R A, Hackler J L and Lawrence K T (1999) The US carbon budget: contributions from land-use change. *Science*, **285**, 574 – 578.
- Hurt G C, Pacala S W, Moorcroft P R, Caspersen J *et al.* (2002) Projecting the future of the US carbon sink. *Proceedings of the National Academy of Sciences*, **99**, 1389 – 1394.
- Oren R *et al.* (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature*, **411**, 469 – 472.
- Pacala S W *et al.* (2001) Consistent land- and atmosphere-based US carbon sink estimates. *Science*, **292**, 2316 – 2420.
- Plattner G, Joos F and Stocker T F (in review) Revision of the global carbon budget due to changing air-sea oxygen fluxes. *Global Biogeochemical Cycles*.

Prentice I C *et al.* (2001) The carbon cycle. In: *Climate Change 2001: The Scientific Basis. Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Houghton J T and Yihui D (Eds). Cambridge University Press, Cambridge.

Schlesinger W H and Lichter J (2001) Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO₂. *Nature*, **411**, 466 – 469.

Websites

www.whrc.org/science/carbon/carbon.htm

Information on Understanding the Global Carbon Cycle from the Woods Hole Research Center

www.wri.org/wri/climate/sinks.html

Information on Carbon sinks and sequestration from the World Resources Institute.

cdiac2.esd.ornl.gov/index.html

Information on Carbon Sequestration from the Office and Science homepage on the US Department of Energy.

Richard A Houghton is a senior scientist at The Woods Hole Research Center. He has been engaged for more than 20 years in reconstructing historic changes in land use and determining associated emissions and sinks of carbon.

Woods Hole Research Center

PO Box 296

Woods Hole, MA 02543

USA

rhoughton@whrc.org

STARTING A BUSINESS?



**INSTITUTE
OF BIOLOGY**

The thought of going into business for yourself is both tempting and terrifying. If you are contemplating starting out on your own, whether as a sole trader, partnership or company, don't miss this course.

The Institute of Biology brings you expert advice and insight from a panel of consultants. Subjects covered include marketing, tax and accounting, as well as other topics to consider when setting up a business.

A one day course, based at the Institute of Biology, will run on **Thursday 12 September 2002. A discount is available to members of the Institute of Biology, non-members are also welcome.**

For booking forms and information on fees, please contact Amy Seales, Conference and Events Manager, Institute of Biology, 20 Queensberry Place, London, SW7 2DE, UK. Email: a.seales@iob.org. Tel: 020 7531 3333 x 257.

www.iob.org