A Primer on the Terrestrial Carbon Cycle: What We Don't Know, But Should

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Abstract

Terrestrial ecosystems are a vital part of the global carbon cycle. . Carbon storage in the terrestrial biosphere is determined from the balance between net primary productivity (the accumulation of carbon through photosynthesis, minus plant respiration) and carbon losses through decomposition, fires, land use and other disturbances. At times when productivity exceeds the sum of decomposition, disturbances and land use, there is a net *sink* of carbon from the atmosphere into ecosystems. When productivity is less than the sum of the other terms, there is a net *source* from ecosystems to the atmosphere.

The scientific community currently believes that the terrestrial biosphere has been acting, on average, as a *net sink* of atmospheric carbon. However, the breakdown between terrestrial carbon sources (from land use and, possibly, the effects of recent climate changes) and terrestrial sinks (from CO_2 or nitrogen fertilization, ecosystem recovery from past land use, shifting forest practices, or changing disturbance patterns) remains unclear. In fact, different estimates of terrestrial ecosystem carbon sources and sinks currently vary by a factor of two.

Understanding the terrestrial carbon budget is not just a matter of proper accounting. It is fundamentally important that we understand the processes underlying terrestrial sources and sinks. For example, if the terrestrial sink is caused from shifting forest practices or the recovery of ecosystems from past land use, then one might reasonably expect the sink to diminish, and even stop, in the not-too-distant future. However, if the terrestrial sink is caused by changes in atmospheric chemistry (such as CO_2 or nitrogen fertilization), then the sink may continue well into the future. In order to accurately forecast changes in future climate, we must understand the dynamics of carbon sources and sinks within the terrestrial biosphere.

Introduction

The terrestrial biosphere is an integral component of the global carbon cycle. Carbon is brought into the terrestrial biosphere through photosynthesis, and it is released back to the atmosphere through plant respiration, microbial respiration (or "decomposition"), fires and some human land use practices. At times when photosynthesis exceeds the sum of plant respiration, microbial respiration, fires and land use releases, there is a net *sink* of carbon from the atmosphere into ecosystems. When photosynthesis is less than the sum of the other terms, there is a net *source* from ecosystems to the atmosphere.

On seasonal timescales, we see the gain and loss of carbon in terrestrial ecosystems through subtle changes in atmospheric CO_2 concentrations – the seasonal "wiggles" in the Mauna Loa curve are a famous example of this phenomenon. But it is on longer timescales, from decades to centuries, that the carbon cycle of the terrestrial biosphere can significantly affect the CO_2 levels in the atmosphere and become important to the climate system. On these longer timescales, the amount of carbon stored in the terrestrial biosphere is the result of the balance between net primary productivity (the net accumulation of carbon through photosynthesis minus plant respiration over a year) and carbon losses through decomposition, land use, fires, and other disturbances (Figure 1).

The scientific community currently believes that the terrestrial biosphere has been acting, on average, as a *net sink* of atmospheric carbon. In fact, terrestrial ecosystems appear to be absorbing a significant fraction of anthropogenic CO_2 emissions (from fossil fuel combustion and, to lesser extent, cement production) during the last few decades – thereby keeping atmospheric CO_2 levels lower than they would otherwise be. The terrestrial biosphere, in effect, has been "subsidizing" part of our fossil fuel emissions – keeping a significant part of these CO_2 emissions out of the atmosphere.

We can consider some basic numbers to illustrate the point. During the decade of the 1990s, human activities were releasing roughly 6 billion tons of carbon per year from fossil fuel combustion and cement production (*Prentice et al.*, 2001). During the same time period, humans may have been releasing another 1-2 billion tons of carbon each year through land use practices, primarily tropical deforestation (*Houghton*, 2000). Taken together, these fossil fuel and land use carbon emissions should lead to a 7-8 billion ton increase in the carbon content of the atmosphere every year. However, observations of atmospheric CO_2 levels shows that only about half of this anthropogenic carbon is accumulating in the atmosphere – the so-called "airborne fraction". The other half of the anthropogenic carbon emissions is, for the time being, apparently absorbed in the oceans and terrestrial biosphere (*Bousquet et al.*, 2000; *Prentice et al.*, 2001; *Schimel et al.*, 2001).

Recent analyses have attempted to determine the fate of anthropogenic CO_2 emissions in the atmosphere, oceans and terrestrial biosphere. There is now overwhelming evidence to suggest that the oceans and terrestrial biosphere together absorb nearly 2 to 3 billion tons of anthropogenic carbon emissions per year – and we can begin to estimate the approximate breakdown between oceanic and terrestrial uptake. For example, in the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), *Prentice et al.* reported that the terrestrial biosphere has been absorbing roughly 1.4 billion tons of carbon per year (or about 22% of the anthropogenic emissions) during the 1990s and nearly 0.2 billion tons of carbon per year (or about 4% of the anthropogenic emissions) in the 1980s (*Prentice et al.*, 2001; Table 1).

	1980s	**1990s**
Measured Increase in Atmospheric CO_2 Levels	3.3 ± 0.1	3.2 ± 0.1
Anthropogenic Emissions from Fossil Fuels and Cement Production	5.4 ± 0.3	6.4 ± 0.4
Net Ocean-Atmosphere Flux of Carbon	-1.9 ± 0.6	-1.7 ± 0.5
Net Land-Atmosphere Flux of Carbon (including all sources from the land, such as tropical deforestation, as well as all land-based carbon sinks)	**-0.2 ± 0.7**	**-1.4 ± 0.7**

Table 1. Estimates of global budget of anthropogenic carbon emissions, as reported by the IPCC Third Assessment Report (*Prentice et al.,* 2001). Units are in billions of tons of carbon per year – or Pg-C (10^{15}g of carbon) per year.

But how certain are these estimates? Even if we can roughly estimate the uptake of CO_2 by terrestrial ecosystems and the oceans, we do not know how these will change in the future. And as we continue to pump more and more CO_2 into the atmosphere, we need to remember that *the terrestrial biosphere may not always continue to absorb such a large share of our emissions*. For example, what if the terrestrial biosphere stopped absorbing so much of our emissions? Or what if the terrestrial biosphere started to *release* carbon dioxide instead of absorbing it? In order to address these questions, we need to understand what controls the uptake of carbon in the terrestrial biosphere.

How Well Can We Estimate the Size of the Terrestrial Sources and Sinks?

In the IPCC Third Assessment Report, *Prentice et al*. reported estimates of the *net* uptake of anthropogenic carbon emissions by the terrestrial biosphere: this includes the balance of all terrestrial carbon *sources* (from deforestation and other land use practices) and all terrestrial carbon *sinks* (the so-called "residual terrestrial sink" or "missing sink").

The estimates of *net* terrestrial carbon uptake show considerable changes in the last two decades: from -0.2 (±0.7) Pg-C yr^{-1} during the 1980s to -1.4 (±0.7) Pg-C yr^{-1} during the 1990s (*Prentice et al*., 2001). These figures were largely estimated using two factors: (1) overall constraints on the global carbon budget (by subtracting the measured atmospheric increase from the total anthropogenic emissions, which are both thought to be reliable estimates, to give the combined uptake of the oceans and terrestrial biosphere); and (2) the break-down of oceanic versus terrestrial carbon uptake as indicated through simultaneous measurements of CO_2 and O_2 in the atmosphere, measurements of $\delta^{13}C$ in the atmosphere, and the results of ocean carbon cycle models (see Appendix 1). *LeQuéré et al*. (2003) have recently updated the *Prentice et al*. estimates of oceanic and terrestrial carbon sinks, and produce new figures for the net terrestrial carbon uptake during the 1980s (-0.3 ± 0.9 Pg-C yr-1) and the 1990s (-1.2 ±0.8 Pg-C yr^{-1}).

In order to determine why there are such large differences in net terrestrial uptake between the 1980s and 1990s, and how this may change in the future, we must break down this *net* uptake value into the different *sources* and *sinks* of atmospheric carbon within terrestrial ecosystems.

Estimating the Size of Terrestrial Carbon Sources

It is presumed that land use practices, such as tropical deforestation and continued agricultural production in temperate latitudes, may lead to the loss of carbon from ecosystems. In particular, slash and burn agricultural practices seen in the tropics (where primary forests are cleared to make way for pastures and croplands) may lead to a substantial source of carbon to the atmosphere.

In a series of keystone papers, *Houghton* and his colleagues estimated the changes in terrestrial carbon balance associated with historical patterns of land use and land cover change (*Houghton et al*., 1983; *Houghton*, 1999, 2003). These estimates are based on national land use inventories (using historical data collected for each region, including agricultural census records reported to the United Nations Food and Agricultural

Organization) and a simple "book-keeping" model of ecosystem carbon cycling. In *Houghton's* book-keeping model, changes in land use and land cover drive changes in terrestrial carbon storage through a series of heuristic rules of how ecosystem carbon pools (including vegetation and soil) respond to land use practices. Furthermore, the carbon removed from terrestrial ecosystems (*e.g.,* wood products, agricultural products) is tracked and allowed to decompose or oxidize back to the atmosphere on timescales ranging from 1 to 100 years.

Houghton's estimates of carbon emissions from land use and land cover change have been used extensively in global budgets of anthropogenic carbon. For the 1980s, *Houghton* estimated that land use and land cover change released roughly 2.0 billion tons of carbon into the atmosphere each year (*Houghton*, 1999). This result implies that there is a large sink of carbon in the terrestrial biosphere – in order to make the net land-atmosphere flux balance out to only –0.2 billion tons per year. In particular, accounting for *Houghton's* land use emissions estimates implies that there was a "residual" terrestrial sink of nearly –2.2 billion tons of carbon per year during the 1980s (see Table 2) (*Prentice et al.*, 2001; *House et al.,* 2003).

1980s Carbon Fluxes	**Houghton Budget**
Atmospheric Increase	3.3
Anthropogenic Emissions	5.4
Net Ocean-Atmosphere Flux	-1.9
Net Land-Atmosphere Flux	-0.2
- *Modeled Land Use Emissions*	*2.0*
- *Implied Residual Terrestrial Sink*	*-2.2*

Table 2. Comparison of global budget of anthropogenic carbon emissions for the 1980s, using Houghton (1999) land use emissions estimates. Units are in billions of tons of carbon per year – or Pg-C (10^{15}g of carbon) per year.

These estimates of terrestrial carbon sources (~2 billion tons per year from land use) and terrestrial carbon sinks (~2.2 billion tons per year accumulating in ecosystems – the so-called “missing sink”) have formed the foundation for our understanding of the global carbon cycle during much of the last decade.

In considering this estimate of the global carbon budget, we find that several terms have a higher degree of certainty than others. For example, there are several different estimates of the atmospheric increase of CO_2 (~3.3 billion tons of carbon per year during the 1980s) and the fossil-fuel emissions rate (~5.4 billion tons of carbon per year during the 1980s): these are probably the “best known” terms in the global carbon budget. Furthermore, the partitioning of the *net* flux of carbon into the oceans and terrestrial biosphere is well constrained by CO_2, O_2 and and $\delta^{13}C$ measurements (see Appendix 1). In addition, the uptake of carbon by the oceans has been estimated by a number of different ocean models, which generally agree with the observation-based budget estimates. *As a result, the most uncertain aspect of the anthropogenic global carbon budget is the breakdown of terrestrial sources (from land use) and terrestrial sinks (the so-called residual or “missing” sink).*

Until very recently, *Houghton's* results were the only available estimates of land use emissions. But in the last few years, a few independent estimates of this part of the carbon cycle have been put forward. One of these new estimates was produced by the Carbon Cycle Model Linkages Project (*CCMLP*) (*McGuire et al.,* 2001).

CCMLP aimed to evaluate the possible mechanisms behind terrestrial carbon sources *and* sinks – using a variety of new modeling tools and datasets (*McGuire et al.*, 2001). In particular, *CCMLP* used four different process-based terrestrial ecosystem models driven by a combination of historical climate, CO_2 and land use data. One of the most novel aspects of this study was the use of the newly-available historical land use data from *Ramankutty and Foley* (1999), which presented estimates of the extent of agricultural land on a 0.5˚ by 0.5˚ gridcell (about ~50 km on a side) for each year from 1700 to 1992.

CCMLP exercised the model in three different ways, each considering different combinations of drivers of terrestrial carbon dynamics: (1) CO_2 changes only; (2) CO_2 and climate changing together; and (3) land use, CO_2 and climate all changing together. These three simulations were conducted with four different models, each running from the mid-1800s to the early 1990s (*McGuire et al.,* 2001).

Considering only the emissions of CO_2 from land use and land cover change during the 1980s, the *CCMLP* results were dramatically different from *Houghton's*. *Houghton* (1999) estimated that land use practices released approximately 2 billion tons of carbon per year during the 1980s, while *CCMLP* (using four different models) estimated a range of land use emissions from 1.0 to 1.7 billion tons of carbon per year (or 50% to 85% of *Houghton's* estimate).

Using these two different estimates for land use emissions in the global carbon budget, we see that there is a major difference in the two terrestrial terms. With *Houghton's* land use emissions estimate, the implied "residual" terrestrial carbon sink is roughly 2.2 billion tons of carbon per year. However, using the *CCMLP* estimates of land use emissions, the implied "residual" sink ranges from 1.2 to 1.9 billion tons of carbon per year (Table 3) (*House et al.,* 2003; *Prentice et al.*, 2001; *McGuire et al.*, 2001).

1980s Carbon Fluxes	**Houghton Budget**	**CCMLP Budget**
Atmospheric Increase	3.3	3.3
Anthropogenic Emissions	5.4	5.4
Net Ocean-Atmosphere Flux	-1.9	-1.9
Net Land-Atmosphere Flux	-0.2	-0.2
- Modeled Land Use Emissions	*2.0*	*1.0 to 1.7*
- Implied Residual Terrestrial Sink	*-2.2*	*-1.2 to -1.9*

Table 3. Comparison of global budget of anthropogenic carbon emissions for the 1980s, using two different estimates of land use emissions – *Houghton* (1999) and *CCMLP* (see *McGuire et al.*, 2001; *Prentice et al.*, 2001; *House et al.*, 2003). It should be noted that *CCMLP* estimated carbon emissions of 0.6-1.0 Pg-C yr^{-1} due to cropland changes alone. We scale this by 60% (the ratio of Houghton's cropland emissions to total land use

emissions), to estimate a *CCMLP* total land use flux of 1.0-1.7 Pg-C yr^{-1}. Units are in billions of tons of carbon per year – or Pg-C (10^{15}g of carbon) per year.

To date, there is no conclusive evidence for why the *Houghton* and *CCMLP* estimates of land use emissions (and the implied "residual" sink of terrestrial ecosystems) are so different. The differences could lie in the underlying land use data (for example, *Ramankutty and Foley* used the cropland area estimates from the U.N. FAO database, while *Houghton* estimated cropland changes based on other deforestation statistics) or in the way that carbon flows through ecosystems were simulated (*Houghton* used a book-keeping model for several large regions of the world, while *McGuire et al.* used four process-based ecosystem models on each 0.5˚ by 0.5˚ gridcell of the world). These two groups are currently working together to understand the differences in the two estimates, and how they can be reconciled in the future (e.g., *House et al.,* 2003).

Two other recent studies (*DeFries et al.,* 2002; *Archard et al.,* 2002) also call into question the original land use emissions estimates of *Houghton*. *DeFries et al*. estimated that land use emissions were ~0.6 (0.3 to 0.8) billion tons of carbon per year in the 1980s (compared to *Houghton's* estimate of 2 billion tons per year), and ~0.9 (0.5 to 1.4) billion tons of carbon per year in the 1990s (compared to *Houghton's* estimate of 2.2 billion tons per year). A similar estimate was produced by *Archard et al*., who suggested land use emissions were 1.0 (±0.2) billion tons of carbon per year during the 1990s. While the *CCMLP*, *DeFries et al*. and *Archard et al*. estimates all seem to point to significantly lower land use emissions than *Houghton*, it is still unclear which estimate is the most accurate.

At this point, it is most important to recognize this: *we may have constrained the overall <u>net</u> flux of carbon between terrestrial ecosystems and the atmosphere (using atmospheric measurements of CO_2, O_2 and ^{13}C – see Prentice et al., 2001), but the breakdown between terrestrial carbon sources (from land use) and terrestrial carbon sinks is still highly uncertain – and possibly in error by a factor of two*.

Estimating the Size of Terrestrial Carbon Sinks

In most early summaries of the global carbon budget, the size of the terrestrial sink was determined by difference. That is, estimates of land use emissions (typically from *Houghton's* studies) were subtracted from the net uptake of the terrestrial biosphere inferred from atmospheric measurements (*e.g.,* Table 2, Table 3). That is, the terrestrial carbon sink was inferred from the difference of other fluxes – and was not described explicitly. This is why it was (until recently) usually referred to as the residual or "missing" sink – or the sink required to "balance the books" of the global carbon cycle.

But the *CCMLP* exercise simulated *both* terrestrial carbon sources (from land use) *and* potential terrestrial carbon sinks. The *CCMLP* models assumed that terrestrial sinks may have resulted from a combination of three factors: (1) ecosystem recovery land use / land cover change; (2) the effects of increasing CO_2 concentrations on plant productivity (the so-called "CO_2 fertilization effect"); and (3) the effects of recent climate variability and climatic change on ecosystems. However, the *CCMLP* study did not include the potential effects of other ecological drivers, such as changing nitrogen deposition, forest management practices, or fire disturbances.

It is worthwhile to note that the *CCMLP* exercise was based on process-based terrestrial ecosystem models. These models use, to the extent possible, a "first principles" approach to simulating ecological and biogeochemical processes. The models generally include detailed calculations of ecosystem physiological processes (including photosynthesis, plant respiration and microbial respiration), as well as heuristic representations of vegetation dynamics and disturbances. The models used in the *CCMLP* activity have also been tested against a wide variety of data, including: *in situ* measurements of carbon and water fluxes, primary productivity and soil moisture balance; satellite-based measurements of vegetation cover and plant phenology; and (by linking the output the ecosystem models to atmospheric transport models) measurements of seasonal atmospheric CO_2 concentrations gathered across the globe. While many deficiencies still exist in the models, they represent our current understanding of how terrestrial ecosystems work, and how they respond to climate, land use, and changing atmospheric chemistry.

As illustrated in Appendix 2, terrestrial carbon sinks can be generated through a variety of different mechanisms: (1) those that increase ecosystem productivity; (2) those that increase the residence time of carbon in vegetation, litter or soil; and (3) those that change the loss of carbon through disturbances (both natural or anthropogenic). While there is still a running debate on the relative importance of these different processes, the *CCMLP* simulations considered the possible carbon sinks associated with CO_2 fertilization (through enhancing NPP), climatic variability (through changes in NPP and residence time of carbon) and land use / land cover change (through changes in the average carbon residence time).

In the *CCMLP* results, the simulated *net* uptake of carbon for the 1980s was roughly -0.3 to -1.5 billion metric tons (*McGuire et al.,* 2001). This range of estimates is in rough agreement (albeit on the high side) with net land-atmosphere flux estimates derived from atmospheric measurements and ocean modeling studies (*Prentice et al.,* 2001; *House et al.,* 2003) – see Figure 2.

The *CCMLP* results can be broken down into their individual components:

CCMLP Terrestrial Carbon Fluxes, 1980s	**Flux Estimates**
Net land-atmosphere flux	**-0.3 to -1.5**
source from cropland change	+0.6 to +1.0
sink from CO_2 fertilization	-1.5 to -3.1
sink from climatic variability	-0.2 to +0.9

Table 4. Breakdown of the terrestrial carbon budget for the 1980s, based on the CCMLP simulations (see McGuire *et al*., 2001; *Prentice et al*., 2001; House *et al*., *in press*). Units are in billions of tons of carbon per year – or Pg-C (10^{15}g of carbon) per year. Note that this reports only the changes in carbon fluxes from *cropland* change, not all land use changes.

These results suggest that these two factors (ecosystem recovery from past land use, and CO_2 fertilization) could be responsible for the "missing" terrestrial carbon sink. Climatic variability actually appears to stimulate (on average) a net source of carbon from terrestrial ecosystems during the 1980s. Other processes not included in the *CCMLP* study – including increasing nitrogen deposition, shifting disturbances and changing forest practices – may also be partly responsible for the sink. Interestingly, this "multi-factor" explanation of the terrestrial carbon sink differs greatly from the explanation offered during the 1970s and 1980s – that the terrestrial carbon sink resulted only from the effects of CO_2 fertilization (see *Sabine et al.*, this volume).

Here, it is important to remember two things. First, *process-based ecosystem models are able to mimic the magnitude and timing (between the 1980s and 1990s) of the net land-atmosphere carbon flux, assuming that carbon sources are driven by land use and climatic variability, and carbon sinks are driven by ecosystem recovery from past land use and* CO_2 *fertilization*. Second, *this does not mean that these mechanisms have actually been "proven" to be responsible for the terrestrial carbon sink*. The models are still largely based on local- to regional-scale representations of ecological processes, and have only had limited testing against global data. Further work is needed to rigorously test different hypothesis regarding the generation of carbon sources and sinks in the terrestrial biosphere.

Summary and Future Challenges

The observed increase in atmospheric CO_2 results from direct anthropogenic carbon emissions and small imbalances in the natural carbon fluxes between the atmosphere, terrestrial biosphere, and oceans (*Prentice et al.*, 2001). Globally, it appears that the terrestrial biosphere is acting as a net sink of carbon (*Prentice et al.*, 2001). But, on a region-by-region basis, terrestrial ecosystems may act as a net source or sink of atmospheric CO_2, depending on the place in question (e.g., *Dixon et al.*, 1994; *McGuire et al.*, 2001; *Prentice et al.*, 2001).

Terrestrial ecosystems are both a source and a sink of atmospheric carbon. On one hand, humans are releasing CO_2 from the terrestrial biosphere through deforestation, cultivation and other land use practices (*Houghton*, 1999; *McGuire et al.*, 2001). In addition, the effects of climate variability and climatic change on terrestrial ecosystems may be causing an additional source of carbon to the atmosphere (*McGuire et al.,* 2001). On the other hand, a significant sink of atmospheric carbon in the terrestrial biosphere may result from several processes – CO_2 fertilization, land use recovery, changing patterns of disturbance or forest harvest, or nitrogen fertilization.

At this stage, it is not clear what the exact magnitude of terrestrial carbon sources and carbon sinks is: estimates vary as much as by a factor of two. Furthermore, we do not yet have a completely satisfactory explanation for the mechanisms of the terrestrial carbon sink. While hypotheses have been put forward, there is still no "smoking gun" that clearly identifies one (or a combination) of these mechanisms as the culprit. A combination of large-scale observations, process-based modeling, ecosystem experimentation and laboratory investigations is still needed to explain the "missing" terrestrial carbon sink.

Only until we understand the size of the terrestrial carbon sources and sinks, and the processes that generate them, can we accurately begin to forecast the future evolution of atmospheric CO_2 (see *Friedlingstein*, this volume). For example, different mechanisms for the terrestrial carbon sink will produce very different future behaviors. If CO_2 fertilization is largely responsible for the terrestrial sink, then the sink might be expected to increase as CO_2 levels continue to rise in the future. However, if the terrestrial sink is being primary caused from the recovery of past land use (*e.g.,* ~50-100 year old abandonment of agriculture in the temperate latitudes), then it is likely that the sink will eventually stop and disappear altogether in a few decades.

This is a fundamental question in understanding the future of the carbon cycle and the climate system: Will the terrestrial carbon sink continue to operate the same way in the future, as climatic changes become larger and larger?

The bottom line is this: *the future evolution of atmospheric CO_2 will not only be determined by human activity, it will also be determined by the terrestrial biosphere and ocean.* In order to accurately forecast changes in future climate, we must understand not only the possible paths of human emissions, but also the dynamics of carbon sources and sinks within the terrestrial biosphere and oceans.

Appendix 1. Methods of Estimating Terrestrial Carbon Fluxes

Here we review some of the methods used to determine the size and geographic locations of terrestrial carbon fluxes. This is just a cursory overview of the topic. In a recent paper, *House et al. (*2003*)* provides a more complete review of the various methods of estimating terrestrial carbon sources and sinks.

Methods for estimating the size and geographic pattern of the terrestrial carbon sink first arose from the so-called "atmospheric inversion" technique of flux estimation. In an inversion method, terrestrial carbon fluxes are inferred by having to fulfill the requirement that the global carbon budget has to be balanced. Thus, knowing the fossil-fuel and land use sources of carbon and the amount of carbon stored in the atmosphere, one can estimate the terrestrial and oceanic sources or sinks by difference. Further, the ocean and terrestrial fluxes can be partitioned by one of three methods: 1) simultaneous measurements of atmospheric CO_2 and O_2; 2) observations of atmospheric $\delta^{13}C$; or 3) oceanic uptake as estimated by an ocean carbon cycle model. The inverse modeling approach has the advantage of being global in scale, and of implicitly accounting for all the processes influencing the global carbon cycle. However, it has the disadvantage of not being able to isolate the individual contributions of the various processes controlling the carbon cycle. Furthermore, while inversion methods are able to provide reasonably accurate estimates of global sources and sinks of carbon, and even sufficiently accurate estimates of the latitudinal north-south partitioning of the fluxes, they do not provide accurate longitudinal breakdown of the fluxes, and of different regional fluxes.

While inversion methods are useful, they are not sufficient to understand the functioning of the terrestrial carbon budget. More direct methods of observing the terrestrial sources and sinks of carbon have been developed. One such observational approach measures terrestrial carbon fluxes at the atmospheric boundary layer in flux towers using the "eddy covariance" technique. This technique takes advantage of the fact that transport in the boundary layer is dominated by turbulent eddies, and uses turbulence theory and sophisticated instruments to measure vertical fluxes of carbon dioxide. While flux measurements are useful to obtain terrestrial fluxes at local scales, they continue to be plagued by measurement errors when turbulence is low (such as at night times), and also have difficulty scaling up to regional levels and to decadal time scales.

Another method of estimating carbon fluxes directly is by using inventory methods. These methods are normally limited to observations of changes in above-ground biomass in forested ecosystems; from changes in biomass, sources or sinks of carbon can be inferred. The method has the advantage of comprehensively including all processes that affect an ecosystem, but has the disadvantage of having limited consideration of belowground processes and non-forested ecosystems.

Finally, various numerical models have been used to estimate terrestrial sources and sinks of carbon. These models include representations of the processes that are thought to affect terrestrial carbon fluxes. In particular, the models include controls such as atmospheric CO_2 concentration, climate variability and change, atmospheric nitrogen deposition, and in a few cases anthropogenic land use and land cover change. The models have the advantage of being able to isolate the individual contributions of the various processes influencing the terrestrial carbon budget. However, the models are only as good as our understanding of the processes, and moreover, they only include the processes that are currently hypothesized to influence the carbon budget.

In addition to all the above approaches to estimating present-day terrestrial carbon fluxes, many experimental approaches are in use to understand how terrestrial ecosystems might respond to changing atmospheric carbon dioxide concentrations and climate. In laboratories, greenhouses, and open top chambers, plants are grown in conditions of increased (or decreased) ambient CO_2 concentrations to evaluate their response. This method has been further extended to the plot or stand scale scale in the Free Air CO_2 Enrichment (FACE) experiments which aims to estimate the ecosystem level response to increased CO_2. Furthermore, many soil warming experiments around the world attempt to measure the response of microbial respiration to increased soil temperatures.

Appendix 2. A Highly Simplified Model of Terrestrial Carbon Balance

In order to consider the mechanisms that may be producing a carbon sink in the terrestrial biosphere, it is useful to consider a highly simplified model of terrestrial carbon dynamics. Using just a few equations, we can describe the flow of carbon from the atmosphere into vegetation, litter and soil carbon pools. Here we use a simplified model based on *Foley* (1995) (Figure 3).

In this highly simplified model, the carbon balance of vegetation can be written as:

$$\frac{\partial C_{v,total}}{\partial t} = \sum_{i=1}^{N} a_i NPP - \sum_{i=1}^{N} \frac{C_{v,i}}{\tau_{v,i}} - D$$

where C_v is the carbon storage within vegetation biomass, *NPP* is the total net primary productivity of the ecosystem, a_i is the allocation coefficient for different vegetation pools (leaves, wood and roots), τ_v is the average residence time of carbon in biomass pools, and *D* is the removal of biomass through disturbances or land use.

When vegetation biomass is lost (through natural turnover or mortality), it is sent to litter – the amount of "dead" carbon that is beginning to decompose – forming CO_2 and soil organic matter. We can represent the carbon balance of the litter pool as:

$$\frac{\partial C_{l,total}}{\partial t} = \sum_{i=1}^{N} \frac{C_{v,i}}{\tau_{v,i}} - \sum_{j=1}^{M} \frac{C_{l,j}}{\tau_{l,j}}$$

where C_l is the carbon content of the litter pools (dead leaves, dead roots and dead wood) and τ_l is the average residence time of carbon in litter.

As litter decays, a fraction of this carbon is immediately lost to the atmosphere as CO_2, while the remaining carbon is converted into soil organic matter (as humus). The carbon balance of the soil carbon pools can be represented as:

$$\frac{\partial C_{s,total}}{\partial t} = (1 - f)\sum_{j=1}^{M}\frac{C_{l,j}}{\tau_{l,j}} - \sum_{k=1}^{P}\frac{C_{s,k}}{\tau_{s,k}}$$

where C_s is the carbon contained in soil organic material (or humus) pools, *(1-f)* is the fraction of the litter that is converted to humus (*f* is how much of the litter is respired to the atmosphere), and τ_s is the average residence time of carbon in soil pools.

When evaluating the overall carbon balance of the terrestrial biosphere, we must consider the carbon budget of the vegetation, litter and soil pools altogether. Looking at these pools together, we see that maintaining a carbon sink in terrestrial ecosystems requires that there must be a net increase in combined carbon mass in the vegetation, litter and soil:

$$\frac{\partial(C_{v,total} + C_{l,total} + C_{s,total})}{\partial t} > 0$$

Reviewing the basic components of our simple terrestrial ecosystem model, we see that that we can produce a carbon sink only when carbon source terms are larger than the carbon loss terms. For example, there can be a sink in vegetation carbon if net primary productivity (NPP) exceeds the loss of carbon (turnover and disturbances). Also, a sink can be produced if the inputs of litter or soil carbon are larger than the losses of carbon through microbial respiration.

In order for the sink to *continue increasing* over time, and continue removing a sizable fraction of increasing CO_2 emissions in the future, the second-derivative of the carbon stocks must also be positive:

$$\frac{\partial^2(C_{v,total} + C_{l,total} + C_{s,total})}{\partial t^2} > 0$$

In order to produce a long-term, sustained sink or source of carbon in terrestrial ecosystems, there must be a mechanism that maintains an imbalance between *NPP*, microbial respiration and other losses of carbon.

One possible way to produce an increasing sink over time include:

$$\frac{\partial NPP}{\partial t} > 0$$

where *NPP* is increasing over time. Or when:

$$\frac{\partial \tau_{v,l,s}}{\partial t} > 0$$

when the average residence time of carbon in vegetation, detritus or soils is increasing.

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Figure Legends.

Figure 1. Relationships between terrestrial, oceanic and atmospheric carbon pools. Adapted from *Foley et al*. (2003).

Figure 2. Estimates of the terrestrial carbon balance. Here the *net carbon balance* of the terrestrial biosphere (as inferred from atmospheric measurements) is presented from *Prentice et al*. (2001). Estimates of land use carbon emissions from *Houghton* are also reported. For comparison, recent modeling estimates of terrestrial carbon balance (arising from combinations of CO_2, climate, and land use change) are shown from the *CCMLP* exercise (*McGuire et al.,* 2001). Figure adapted from *House et al*. (2003).

Figure 3. A highly simplified model of the terrestrial carbon cycle. Here carbon flows from the atmosphere into terrestrial vegetation, then into litter and soil organic matter. Along the way, carbon is lost back to the atmosphere through microbial respiration (or decomposition) of litter and soil organic materials. Adapted from *Foley* (1995).