

Reconciling Carbon-Cycle Concepts, Terminology, and Methods

F.S. Chapin, III^a, G.M Woodwell, J.T. Randerson, E.B. Rastetter, G.M. Lovett, D.D. Baldocchi, D.A. Clark, M.E. Harmon, D.S. Schimel, R. Valentini, C. Wirth, J.D. Aber, J.J. Cole, M.L. Goulden, J.W. Harden, M. Heimann, R.W. Howarth, P.A. Matson, A.D. McGuire, J.M. Melillo, H.A. Mooney, J.C. Neff, R.A. Houghton, M.L. Pace, M.G. Ryan, S.W. Running, O.E. Sala, W.H. Schlesinger, E.-D. Schulze

^a Corresponding author

Abstract. Recent patterns and projections of climatic change have focused increased scientific and public attention on patterns of carbon (C) cycling and its controls, particularly the factors that determine whether an ecosystem is a net source or sink of atmospheric CO₂. Net ecosystem production (NEP), a central concept in C-cycling research, has been used to represent two different concepts by C-cycling scientists. We propose that NEP be restricted to just one of its two original definitions—the imbalance between gross primary production (GPP) and ecosystem respiration (ER), and that a new term—net ecosystem carbon balance (NECB)—be applied to the net rate of C accumulation in (or loss from; negative sign) ecosystems. NECB differs from NEP when C fluxes other than C fixation and respiration occur or when inorganic C enters or leaves in dissolved form. These fluxes include leaching loss or lateral transfer of C from the ecosystem; emission of volatile organic C, methane, and carbon monoxide; and soot and CO₂ from fire. C fluxes in addition to NEP are particularly important determinants of NECB over long time scales. However, even over short time scales, they are important in ecosystems such as streams,

estuaries, wetlands, and cities. Recent technological advances have led to a diversity of approaches to measuring C fluxes at different temporal and spatial scales. These approaches frequently capture different components of NEP or NECB and can therefore be compared across scales only by carefully specifying the fluxes included in the measurements. By explicitly identifying the fluxes that comprise NECB and other components of the C cycle, such as net ecosystem exchange (NEE) and net biome production (NBP), we provide a less ambiguous framework for understanding and communicating recent changes in the global C cycle.

Key words: Net ecosystem production, net ecosystem carbon balance, gross primary production, ecosystem respiration, autotrophic respiration, heterotrophic respiration, net ecosystem exchange, net biome production, net primary production.

Introduction

Carbon (C) constitutes about half the dry mass of life on earth and of the organic matter that accumulates in soils and sediments when organisms die. Its central role in the biogeochemical processes of ecosystems has therefore always been of keen interest to ecosystem ecologists (Lindeman 1942; Odum 1959; Ovington 1962; Rodin and Bazilevich 1967; Woodwell and Whittaker 1968; Fisher and Likens 1973; Lieth 1975). In recent decades an even broader community of scientists and policy makers has become interested in understanding the controls over C cycling, because it has become abundantly clear that the biological and physical controls over C absorption, sequestration, and release by ecosystems strongly influence the CO₂ concentration and heat-trapping capacity of the atmosphere and therefore the dynamics of the

global climate system (Woodwell and Mackenzie 1995; Wigley et al. 1996; Cox et al. 2000; Prentice et al. 2001; Fung et al. 2005). As part of the 1997 Kyoto Protocol to the United Nations Framework Convention on Climate Change, countries may use increases in C storage by ecosystems as one way to meet mandated reductions in C emissions from burning fossil fuels. This has created huge economic and political stakes in understanding the controls over C cycling by ecosystems.

Given the central role of the C cycle in climate change and the breadth of disciplines involved in its study, it is important that C-cycling concepts and terminology be clearly defined. Ecosystems are important sources and sinks of C so it is critical to define unambiguously whether a system or region releases or absorbs CO₂ from the atmosphere. Lovett et al. (Lovett et al. In press) point out that net ecosystem production (NEP), the central term used to describe imbalances in C uptake and loss by ecosystems, has been used to represent two distinct concepts in the C-cycling literature, leading to miscommunication and potential confusion.

In this paper we briefly review some of the historical, methodological, and conceptual roots of the differences in C-cycling questions and approaches and suggest a common framework and terminology for studying the cycling of carbon in ecosystems. Our goal is to clarify concepts and definitions within a common conceptual framework and point out persisting ambiguities that require further research.

Net Ecosystem Production and C Accumulation Rates in Ecosystems

Net ecosystem production (NEP) was initially defined by Woodwell and Whittaker (1968) in two ways: (1) as the difference between ecosystem-level photosynthetic gain of CO₂-C

(gross primary production, GPP) and ecosystem (plant, animal, and microbial) respiratory loss of CO_2 -C (ecosystem respiration, ER) and (2) as net rate of C accumulation in ecosystems. This represented the core of an elegant but simple ecosystem C model in which the rate of C accumulation in an ecosystem resulted from the imbalance of photosynthesis and ecosystem respiration. Earlier Odum (1956) had linked concepts of C cycling and energy flow and pointed out that ecosystems often accumulate C when $\text{GPP/ER} > 1$; autotrophic ecosystems) or lose C when $\text{GPP/ER} < 1$ (heterotrophic ecosystems). In other ecosystems, such as cities and streams, lateral flows of C and energy can be the major determinants of net ecosystem C balance regardless of whether the ecosystem is autotrophic or heterotrophic (Fisher and Likens 1973). This raises questions about the nature of linkages between GPP, ER, and the net accumulation of C in ecosystems.

Woodwell and Whittaker (1968) developed their concept of NEP in the context of a 50-60 year old mid/late successional forest in which photosynthetic gain and ecosystem respiration were assumed to be the dominant fluxes responsible for C accumulation. As a global long-term average, this is a reasonable approximation, because the annual storage of C in soils in chronosequences ≥ 1000 years is only about 0.5% of net primary production (NPP; photosynthesis minus the respiration of primary producers), indicating that various respiratory processes and other loss pathways are quite efficient at burning up organic C (Schlesinger 1990). A similar quantity of C is annually transported by rivers from land to oceans and is balanced by a release of CO_2 from the oceans and subsequent uptake by terrestrial ecosystems, leaving the land close to steady state prior to the Anthropocene (Schlesinger and Melack 1981; Aumont et al. 2001). However, when the concept of NEP is applied to a broad array of ecosystems and time scales, dissolved, volatile, and depositional organic and inorganic C fluxes other than GPP and

ER are often substantial. Therefore, the imbalance between GPP and ER does *not*, as a generality, equal net C accumulation rate in ecosystems (Fisher and Likens 1973; Rosenbloom et al. 2001; Randerson et al. 2002; Lovett et al. In press). In the wake of increasing recognition that GPP minus ER does not equal net C accumulation rate, some authors have defined NEP primarily as net C accumulation rate (Aber and Melillo 1991; Sala and Austin 2000; Chapin et al. 2002; Randerson et al. 2002) and others as the imbalance between GPP and ER (Schlesinger 1997; Howarth and Michaels 2000; Aber and Melillo 2001; Falge et al. 2002), leading to confusion about what NEP estimates in the literature actually represent.

Cursory searches of the phrase “Net Ecosystem Production” in the Web of Science and JSTOR indicate that disciplines differ in their prevailing definition of the term. In general, aquatic and atmospheric scientists have defined NEP as $GPP - ER$, whereas terrestrial ecologists have defined NEP as either the net C accumulation rate or simultaneously as both $GPP - ER$ and the net C accumulation rate. Initial discussions among authors of the present paper revealed similar disagreement about how Woodwell and Whittaker (1968) had initially defined NEP and what this term should represent today. However, if the NEP concept is to be useful in communicating among researchers who study different components of an integrated landscape, scientists must agree on a single definition.

We support the suggestion of Lovett et al. (In press) that NEP be defined as $GPP - ER$. Defined in this way, NEP is conceptually simple and analogous to NPP (photosynthesis minus the respiration of primary producers). It can therefore be unambiguously incorporated into biogeochemical models and is independent of the continually evolving technology of measuring the components of ecosystem C budgets. We propose that **Net Ecosystem Carbon Balance** (NECB) be the term applied to the net rate of C accumulation in (or loss from; negative sign)

ecosystems. NECB represents the overall ecosystem C balance from all sources and sinks—physical, biological, and anthropogenic:

$$\text{NECB} = dC/dt \quad (1)$$

Net fluxes of several forms of C contribute to NECB:

$$\text{NECB} = -\text{NEE} + F_{\text{CO}} + F_{\text{CH}_4} + F_{\text{VOC}} + F_{\text{DIC}} + F_{\text{DOC}} + F_{\text{PC}} \quad (2)$$

where NEE is net ecosystem exchange (the net CO₂ flux from the ecosystem to the atmosphere (or net CO₂ uptake; positive sign); F_{CO} is net carbon monoxide (CO) absorption (or efflux; negative sign); F_{CH₄} is net methane (CH₄) consumption (or efflux; negative sign); F_{VOC} is net volatile organic C (VOC) absorption (or efflux; negative sign); F_{DIC} is net dissolved inorganic C (DIC) input to the ecosystem (or net DIC leaching loss; negative sign); F_{DOC} is net dissolved organic C (DOC) input (or net DOC leaching loss; negative sign); and F_{PC} is the net lateral transfer of particulate (non-dissolved, nongaseous) C into the ecosystem (or out of; negative sign) by processes such as animal movement, soot emission during fires, water and wind deposition and erosion, and anthropogenic transport or harvest. Extrapolation of NECB to larger spatial scales has been termed net biome productivity (NBP) (Schulze and Heimann 1998).

A common conceptual framework

To place NEP and NECB in a common conceptual framework, it is useful to view the ecosystem as a volume with explicitly defined top, bottom, and sides (Randerson et al. 2002) (Fig. 1). In terrestrial ecosystems the top of this defined volume is typically above the canopy and the bottom is below the rooting zone. In aquatic ecosystems the top of the ecosystem is typically the air-water interface (or sometimes the sediment-water interface) and the bottom is either beneath the sediments or somewhere within the water column. In streams and rivers, this ecosystem may be defined with reference to a moving parcel of water or to stationary points in the streambed. NECB equals the total C input minus the total C output from the ecosystem over a specified time interval.

On short time scales, GPP and ER (i.e., the components of NEP) are the processes that typically consume and produce, respectively, most of the inorganic C in an ecosystem. In the light, for example, GPP typically exceeds ER, resulting in a positive NEP. This reduces the concentration of CO₂ and/or DIC inside the ecosystem and generates a diffusion gradient that causes CO₂ to enter the ecosystem from the atmosphere (a negative NEE). Conversely, in the dark, ER typically dominates CO₂ exchange, resulting in a negative NEP. This increases the concentration of CO₂ and/or DIC inside the ecosystem and generates a diffusion gradient that causes CO₂ to move from the ecosystem to the atmosphere (a positive NEE). Thus, over short time scales, GPP and ER are two of the key processes that drive NECB, and [-NEE] often closely approximates both NEP and NECB in many ecosystems (Baldocchi 2003). [Note that, by convention, NEE is opposite in sign to NEP and NECB because NEE is defined by atmospheric scientists as a C input to the atmosphere, whereas NEP and NECB are defined by ecologists as C inputs to ecosystems.]

Nonetheless, different types of ecosystems may be dominated by radically different C fluxes, particularly over the long term. There are several general reasons why [-NEE], NEP, and NECB may diverge from one another.

Because NEE is, by definition, the CO₂ flux from the ecosystem to the atmosphere, [-NEE] diverges from NEP and NECB when inorganic C enters or leaves an ecosystem as DIC in the aquatic phase rather than through atmospheric exchange. Leaching of groundwater, for example, generally transfers respiration-derived DIC from terrestrial to aquatic ecosystems, causing [-terrestrial NEE] to be greater than terrestrial NEP or NECB and [-aquatic NEE] to be less than aquatic NEP or NECB. On short time scales, this discrepancy is often small, but on an annual basis it can be substantial. About 20% of terrestrial NEP in arctic Alaska, for example, is transferred to aquatic ecosystems as DIC (Kling et al. 1991). Similarly, upwelling and other vertical or horizontal mixing of water masses can move DIC among aquatic ecosystems in patterns that are not reflected in NEE.

Because NEP is, by definition, the inorganic C exchange of an ecosystem caused by GPP and ER, NECB diverges from NEP when C enters or leaves ecosystems in forms other than CO₂ or DIC. Other important fluxes include leaching loss from (or input to) the ecosystem of DOC; emission of CH₄, CO, and VOCs; erosion; fire; harvest; and other vertical and lateral C transfers (Schlesinger 1997; Stallard 1998; Guenther 2002; Randerson et al. 2002). In streams, rivers, and estuaries, lateral C transfers among ecosystems often dominate NECB (Fisher and Likens 1973; Howarth et al. 1996; Richey et al. 2002). Some ecosystems with large lateral C imports (e.g., cities, estuaries, and some lakes) can be a net CO₂ source to the atmosphere. In lakes, rivers, and oceans, physical processes such as CO₂ solubility, vertical mixing rates, and sedimentation of particulate organic C (POC) often dominate the C budget (Lovett et al. In press).

NECB also diverges from NEP when inorganic C enters or leaves ecosystems for reasons other than an imbalance between GPP and ER. The largest non-respiratory oxidations of organic matter to inorganic C are by fire in terrestrial ecosystems and by UV radiation in aquatic ecosystems. Some ecosystems accumulate inorganic C (e.g., desert caliche; typically $< 5 \text{ g C m}^{-2} \text{ yr}^{-1}$; Schlesinger 1985) or show small gains in inorganic C associated with weathering of carbonate rocks ($< 3\%$ of NPP) (Andrews and Schlesinger 2001). These inorganic C accumulation rates are captured in NECB but not NEP and are typically small.

The processes responsible for divergence between $[-\text{NEE}]$, NEP, and NECB change with temporal and spatial scale. On century time scales, vegetation development during succession is associated with a positive NEP and NECB (and a negative NEE). During fires, there is a brief time when NEP is zero (no photosynthesis or respiration), but NECB decreases and NEE increases dramatically. Prior to the Anthropocene (Ruddiman 2003), NEP of the terrestrial biosphere as a whole was probably slightly positive, with NPP exceeding heterotrophic respiratory losses. In contrast, NECB was probably closer to being in balance, as dissolved organic and particulate fluxes to the ocean offset some of the positive NEP. During the Pleistocene, variations in the spatial extent of ice sheets across North America and Europe (and their influence on soil formation and erosion) probably contributed to a divergence between NEP and NECP, and would have been one of many factors (along with permafrost and sea level variations) that set the carbon balance of the terrestrial biosphere.

As efforts develop to integrate estimates of NECB across heterogeneous landscapes containing terrestrial, freshwater, and marine ecosystems or to compare measurements made at different temporal scales, it becomes crucial that the same combinations of fluxes are being compared. As a start, the key C fluxes (e.g., GPP, ER, NPP, NEP, and NECB) must have the

same units (e.g., $\text{kg C ha}^{-1} \text{ yr}^{-1}$) and be calculated in a manner that is independent of temporal and spatial scale, so estimates can be readily compared across scales. However, as we have pointed out, different types of ecosystems are dominated by radically different fluxes, and the techniques used to estimate them are quite scale-dependent. Any estimate of NEP or NECB from field observations should therefore specify explicitly which fluxes are included in the estimate and which fluxes are unmeasured or assumed to be negligible.

Clarifying Carbon Cycling Concepts

Although this mini-review focuses on NEP and NECB, similar ambiguities cloud the use of other central concepts in the C cycle. We offer the following conventions in defining some of the central concepts and point out unresolved issues that still complicate the use and interpretation of these terms.

Gross primary production (GPP) is the sum of gross C fixation by autotrophic C-fixing tissues per unit ground or water area and time. Because our emphasis here is on the C budget of ecosystems, we include both photosynthesis and chemoautotrophy in GPP. However, because the energy that drives chemoautotrophy is either completely (reduced substrate plus O_2 or other oxidants in sediments) or partly (O_2 or other oxidants in geothermal vents) derived from photosynthesis, we recognize that from an energetic perspective chemoautotrophy is better classified as a component of secondary production, rather than GPP (Howarth and Teal 1980; Howarth 1984). Although chemoautotrophy is a small component of CO_2 fixation globally, locally it can be a very important component of the C budget (Howarth 1984; Jannasch and Mottl 1985).

Autotrophic respiration (AR) is the sum of respiration (CO_2 production) by all living parts of primary producers per unit ground or water area and time. The extent to which rhizosphere microbes and mycorrhizae contribute to measured “root respiration” is uncertain. It is even unclear whether these root-associated microbial fluxes should be considered part of autotrophic or heterotrophic respiration. Lumping rhizosphere microbes, mycorrhizal fungi, and bacteria of N-fixing nodules with other heterotrophs is conceptually cleaner but their impact on plant nutrition and C balance and the measurement of their respiration rates are difficult to separate from other root functions.

Heterotrophic respiration (HR) is the respiration rate of heterotrophic organisms (animals and microbes) summed per unit ground or water area and time.

Ecosystem respiration (ER) is the respiration of all organisms summed per unit ground or water area and time.

Net ecosystem production (NEP) is GPP minus ER. In pelagic systems of lakes and oceans NEP can be measured directly by enclosing the ecosystem in a jar or measuring diel changes in dissolved oxygen or CO_2 (Howarth and Michaels 2000; Hanson et al. 2003). Interestingly, the measurement of NEP is more robust than calculations of GPP and ER, which depend on the assumption that respiration measured in the light is the same as measured in the dark, a relationship that appears to be variable (Roberts et al. In press).

In contrast to aquatic ecosystems, the structural complexity of terrestrial ecosystems creates challenges for measuring NEP directly, so terrestrial ecologists have focused on estimates of GPP and ER based on gas exchange. Calculation of NEP from these fluxes assumes that foliar respiration and the temperature response of ecosystem respiration during the day are the same as at night. These assumptions are questionable because photorespiration in chloroplasts, which

occurs only in the light, is compensated to an unknown extent by down-regulation of mitochondrial respiration in the light (Kirschbaum and Farquhar 1984) or by the use of the respired CO₂ in photosynthesis (Loreto et al. 1999; Loreto et al. 2001). These uncertainties are analogous to those confronted by aquatic ecologists in calculating GPP and ER from NEP.

Net ecosystem exchange (NEE) is the net CO₂ exchange with the atmosphere, i.e., the vertical and lateral CO₂ flux from the ecosystem to the atmosphere (Baldocchi 2003). There are occasions of high atmospheric stability when CO₂ exchange by the ecosystem may not reach the eddy covariance measurement system; in this case a storage term is added, which is the vertical integral of dC/dt , measured with a CO₂ profile system at two points in time. The storage term can also be used to identify lateral advection, if the build-up of CO₂ in the stand is less than would be expected from soil respiration (Aubinet et al. 2003). When advection occurs, NEE differs from the vertical canopy flux measured by eddy covariance. NEE differs from NEP in being opposite in sign; in omitting gains and losses of respiration-derived DIC; and in including non-respiratory CO₂ fluxes such as those from fire or UV oxidation of organic matter (Fig. 1). NEE approaches NEP (= GPP – ER) (but is opposite in sign), when these other fluxes and changes in inorganic C storage within the ecosystem are small.

Net primary production (NPP) is GPP – AR. NPP includes not only the growth of primary producers (biomass accumulation and tissue turnover above and below ground in terrestrial ecosystems) but also the C transfer to herbivores and root symbionts (e.g., mycorrhizal fungi), the excretion of organic C from algae, and the production of root exudates and plant VOCs (Long et al. 1989; Clark et al. 2001; Kesselmeier et al. 2002). Published summaries of data on terrestrial NPP are, however, usually based on data from litterfall and aboveground biomass accumulation and therefore are not closely aligned to the concept of NPP as the

imbalance between GPP and AR (Clark et al. 2001). Estimates of NPP in aquatic ecosystems based on ^{14}C are intermediate to the theoretical rates of NPP and GPP because phytoplankton respire some but not all of the newly fixed, ^{14}C -labelled organic C (Peterson 1980; Howarth and Michaels 2000).

Net ecosystem carbon balance (NECB) is the net rate of organic plus inorganic C accumulation in (or loss from; negative sign) an ecosystem, regardless of the temporal and spatial scale at which it is estimated. NECB can be measured directly in terrestrial ecosystems, particularly over long time scales, as the change in total C in the ecosystem over the measured time interval. In early successional and managed ecosystems, changes in C stocks may be detectable in years to decades (Matson et al. 1997; Richter et al. 1999), but in most other ecosystems C stocks change too slowly to be detected easily, given their substantial spatial variability.

Net biome production (NBP) is NECB estimated at large temporal and spatial scales. The concept was developed to account for many of the fluxes seldom measured by NEE and explicitly includes disturbances such as fire that remove C from the system via non-respiratory processes in addition to disturbances that redistribute C from the biomass into detrital pools (Schulze and Heimann 1998; Schulze et al. 1999; Schulze et al. 2000). NBP can thus be viewed as the spatial and temporal average of NECB over a heterogeneous landscape:

$$NBP = \frac{\int_T \int_A NECB(x,t) dx dt}{T \cdot A} \quad (3)$$

where A is the land surface area considered, T is the temporal extent of the integration, and x and t are the spatial and temporal coordinates. Because NECB can be estimated at any temporal and spatial scale, it facilitates cross-scale comparisons between short-term flux measurements and long-term C accumulation estimates, whereas NBP applies explicitly to large scales (Schulze et al. 2002; Ciais et al. 2005). One of the greatest challenges in refining the global C budget is to scale from short-term measurements on relatively homogeneous flat terrain to large topographically heterogeneous regions, where long-term C budgets are strongly influenced by spatial interactions among ecosystems (such as lateral air drainage and erosion) and rare events (such fire and insect outbreaks).

Conclusions and Next Steps

The construction of an integrated C budget is challenging because many commonly used methods incorporate some, but not all of the fluxes we have defined above. Lack of data on key ecosystem C fluxes such as root production often lead to incorporation of literature values or model estimates that may or may not be transferable among ecosystems, suggesting the need for caution and redundant approaches in developing C budgets. In addition, some methods contain consistent biases that make it challenging to link with other flux estimates. Lateral air drainage at night can lead to underestimates of night-time ecosystem respiration in eddy covariance measurements (Aubinet et al. 2003). $^{14}\text{CO}_2$ incorporation and gas exchange measurements capture different components of the balance between GPP and AR. Because the estimates obtained for a particular flux depend strongly on the method and time scale of measurement, these should be specified (e.g., hourly GPP, daily AR, annual NPP).

Technological developments further complicate efforts to develop unambiguous C budgets, because new measurement techniques capture different components of ecosystem fluxes from those available when the terminology in use today was first crafted (Fig. 2). Depending on the spatial scale and duration of the measurement program, gas flux-based techniques can capture something that may approximate NEP (for example from a tower in a homogeneous environment with small dissolved, depositional, and erosional fluxes). A larger-scale airborne boundary layer budget in a mosaic of forest and lakes measures the autochthonous components in both systems, and some amount of aquatic respiration of terrestrially fixed C. Regional to global inverse analyses include even larger contributions from respiration of transported C and land use/disturbance fluxes such as from fire (Heimann et al. 1998; Bousquet et al. 2000). The respiration of imported agricultural products, for example, had to be accounted for to interpret Europe's C budget correctly from atmospheric data (Janssens et al. 2003). Most C cycle research gives insufficient attention to C fluxes associated with transported particulate and dissolved C, VOC and methane emissions, disturbance, harvest, and trade. The variable relationships among C cycling rates, oxygen transfers, and energy flow are often overlooked.

The scientific community, managers, and the general public need both clear definitions of the conceptual components of C exchange and clear terms for the fluxes that can be measured. They must understand the relationship among these frequently divergent ways of viewing the carbon cycle. Until concepts are more clearly aligned with measurements, there is a serious risk of misunderstanding or miscommunication about the role of human activities in the biosphere, making it difficult to apply scientific understanding to the practical management of C emissions and sequestration.

Acknowledgments. We thank Gus Shaver, Stuart Fisher, and two anonymous reviewers for their insightful comments.

References

Aber JD, Melillo JM. 1991. *Terrestrial Ecosystems*. Orlando: Saunders College Publishing.

Aber JD, Melillo JM. 2001. *Terrestrial Ecosystems, Second Edition*. San Diego: Harcourt-Academic Press.

Andrews JA, Schlesinger WH. 2001. Soil CO₂ dynamics, acidification, and chemical weathering in a temperate forest with experimental CO₂ enrichment. *Global Biogeochemical Cycles* 15:149-162.

Aubinet M, Heinesch B, Yernaux M. 2003. Horizontal and vertical CO₂ advection in a sloping forest. *Boundary Layer Meteorology* 108:397-417.

Aumont O et al. 2001. Riverine-driven interhemispheric transport of carbon. *Global Biogeochemical Cycles* 15:393-405.

Baldocchi DD. 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology* 9:479-492.

Bousquet P, Peylin P, Ciais P, Le Quere C, Friedlingstein P, Tans PP. 2000. Regional changes in carbon dioxide fluxes of land and oceans since 1980. *Science* 290:1342-1346.

Chapin FS, III, Matson PA, Mooney HA. 2002. *Principles of Terrestrial Ecosystem Ecology*. New York: Springer-Verlag.

- Ciais P et al. 2005. The potential for rising CO₂ to account for the observed uptake of carbon by tropical, temperate and boreal forest biomes. Griffith H, Jarvis P, editors. *The Carbon Balance of Forest Biomes*. Milton Park, UK: Taylor and Francis. p 109-150.
- Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J. 2001. Measuring net primary production in forests: Concepts and field methods. *Ecological Applications* 11:356-370.
- Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408:184-187.
- Falge E et al. 2002. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agricultural and Forest Meteorology* 113:53-74.
- Fisher SG, Likens GE. 1973. Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. *Ecological Monographs* 43:421-439.
- Fung IY, Doney SC, Lindsay K, John J. 2005. Evolution of carbon sinks in a changing climate. *Proceedings of the National Academy of Science* 102:11201-11206.
- Guenther A. 2002. The contribution of reactive carbon emissions from vegetation to the carbon balance of terrestrial ecosystems. *Chemosphere* 49:837-844.
- Hanson PC, Bade DL, Carpenter SR, Kratz TK. 2003. Lake metabolism: Relationships with dissolved organic carbon and phosphorus. *Limnology and Oceanography* 48:1112-1119.
- Heimann M et al. 1998. Evaluation of terrestrial carbon cycle models through simulations of the seasonal cycle of atmospheric CO₂: First results of a model intercomparison study. *Global Biogeochemical Cycles* 12:1-24.
- Howarth RW. 1984. The ecological significance of sulfur in the energy dynamics of salt marsh and marine sediments. *Biogeochemistry* 1:5-27.

- Howarth RW, Michaels AF. 2000. The measurement of primary production in aquatic ecosystems. Sala OE, Jackson RB, Mooney HA, Howarth RW, editors. *Methods in Ecosystem Science*. New York: Springer-Verlag. p 72-85.
- Howarth RW, Schneider R, Swaney D. 1996. Metabolism and organic carbon fluxes in the tidal, freshwater Hudson River. *Estuaries* 19:848-865.
- Howarth RW, Teal JM. 1980. Energy flow in a salt marsh ecosystem: The role of reduced inorganic sulfur compounds. *American Naturalist* 116:862-872.
- Jannasch HW, Mottl MJ. 1985. Geomicrobiology of deep-sea hydrothermal vents. *Science* 229:717-725.
- Janssens IA et al. 2003. Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic CO₂ emissions. *Science* 300:1538-1542.
- Kesselmeier J et al. 2002. Volatile organic compound emissions in relation to plant carbon fixation and the terrestrial carbon budget. *Global Biogeochemical Cycles* 16:Art. No. 1126.
- Kirschbaum MUF, Farquhar GD. 1984. Temperature dependence of whole-leaf photosynthesis in *Eucalyptus pauciflora* Sieb. ex Spreng. *Australian Journal of Plant Physiology* 11:519-538.
- Kling GW, Kipphut GW, Miller MC. 1991. Arctic lakes and streams as gas conduits to the atmosphere: Implications for tundra carbon budgets. *Science* 251:298-301.
- Lieth H. 1975. Modeling the primary productivity of the world. Lieth H, Whittaker RH, editors. *Primary Productivity of the Biosphere*. Berlin: Springer-Verlag. p 237-263.
- Lindeman RL. 1942. The trophic-dynamic aspects of ecology. *Ecology* 23:399-418.

- Long SP et al. 1989. Primary productivity of natural grass ecosystems of the tropics: A Reappraisal. *Plant and Soil* 115:155-166.
- Loreto F, Delfine S, Di Marco G. 1999. Estimation of photorespiratory carbon dioxide recycling during photosynthesis. *Australian Journal of Plant Physiology* 26:733-736.
- Loreto F, Velikova V, Di Marco G. 2001. Respiration in the light measured by (CO₂)-C-12 emission in (CO₂)-C-13 atmosphere in maize leaves. *Australian Journal of Plant Physiology* 28:1103-1108.
- Lovett GM, Cole JJ, Pace ML. In press. Is net ecosystem production equal to ecosystem carbon storage? *Ecosystems*.
- Matson PA, Parton WJ, Power AG, Swift MJ. 1997. Agricultural intensification and ecosystem properties. *Science* 227:504-509.
- Odum EP. 1959. *Fundamentals of Ecology*. Philadelphia: W. B. Saunders.
- Odum HT. 1956. Primary production in flowing waters. *Limnology and Oceanography* 1:102-117.
- Ovington JD. 1962. Quantitative ecology and the woodland ecosystem concept. *Advances in Ecological Research* 1:103-192.
- Peterson BJ. 1980. Aquatic primary productivity and the ¹⁴C-CO₂ method: A history of the productivity problem. *Annual Review of Ecology and Systematics* 11:359-385.
- Prentice IC et al. 2001. The carbon cycle and atmospheric carbon dioxide. Houghton JT et al., editors. *Climate Change 2001: The Scientific Basis*. Cambridge: Cambridge University Press. p 183-237.

- Randerson JT, Chapin FS, III, Harden J, Neff JC, Harmon ME. 2002. Net ecosystem production: A comprehensive measure of net carbon accumulation by ecosystems. *Ecological Applications* 12:937-947.
- Richey JE, Melack JM, Aufdenkampe AK, Ballester VM, Hess LL. 2002. Outgassing from Amazonian rivers and wetlands as a large tropical source of atmospheric CO₂. *Nature* 416:617-620.
- Richter DD, Markewitz D, Trumbore SE. 1999. Rapid accumulation and turnover of soil carbon in a reestablishing forest. *Nature* 400:56-58.
- Roberts BJ, Owens TG, Ostrom NE, Howarth RW. In press. Aquatic ecosystem respiration rates are not constant over diel cycles: Direct quantification using dissolved oxygen concentration and isotopic composition in experimental ponds. *Limnology and Oceanography*
- Rodin LE, Bazilevich NI. 1967. *Production and Mineral Cycling in Terrestrial Vegetation*. Edinburgh, Scotland: Oliver and Boyd.
- Rosenbloom NA, Doney SC, Schimel DS. 2001. Geomorphic evolution of soil texture and organic matter in eroding landscapes. *Global Biogeochemical Cycles* 15:365-381.
- Ruddiman WF. 2003. The anthropogenic greenhouse era began thousands of years ago. *Climatic Change* 61:261-293.
- Sala OE, Austin AT. 2000. Methods of estimating aboveground net primary productivity. Sala OE, Jackson RB, Mooney HA, Howarth RW, editors. *Methods in Ecosystem Science*. New York: Springer-Verlag. p 31-43.
- Schlesinger WH. 1985. The formation of caliche in soils of the Mojave Desert, California. *Geochimica et Cosmochimica Acta* 49:57-66.

- Schlesinger WH. 1990. Evidence from chronosequence studies for a low carbon-storage potential of soils. *Nature* 348:232-234.
- Schlesinger WH. 1997. *Biogeochemistry: An Analysis of Global Change*, Second edn. San Diego: Academic Press.
- Schlesinger WH, Melack JM. 1981. Transport of organic carbon in the world's rivers. *Tellus* 33:172-187.
- Schulze E-D, Heimann M. 1998. Carbon and water exchange of terrestrial systems. Hallway JN, Melillo J, editors. *Asian change in the context of global change*. Cambridge: Cambridge University Press. p 145-161.
- Schulze E-D et al. 1999. Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink--a synthesis. *Global Change Biology* 5:703-722.
- Schulze E-D, Wirth C, Heimann M. 2000. Climate change: Managing forests after Kyoto. *Science* 289:2058-2059.
- Schulze E-D, Wirth C, Heimann M. 2002. Carbon fluxes of the Eurosiberian Region. *Environmental Control in Biology* 40:249-258.
- Stallard RF. 1998. Terrestrial sedimentation and the carbon cycle: Coupling weathering and erosion to carbon burial. *Global Biogeochemical Cycles* 12:231-257.
- Wigley TML, Richels R, Edmonds JA. 1996. Economic and environmental choices in the stabilization of atmospheric CO₂ concentrations. *Nature* 379:240-243.
- Woodwell GM, Mackenzie FT, Woodwell GM, Mackenzie FT, Woodwell GM, Mackenzie FTs. 1995. *Biotic Feedbacks in the Global Climatic System: Will the Warming Feed the Warming?* New York: Oxford University Press.

Woodwell GM, Whittaker RH. 1968. Primary production in terrestrial communities. *American Zoologist* 8:19-30.

Figure legends

Fig. 1. Relationship among carbon (C) fluxes that determine Net Ecosystem Carbon Balance (NECB—the net of all C imports to and exports from the ecosystem) and fluxes (in bold) that determine Net Ecosystem Production (NEP). The box represents the ecosystem. Fluxes contributing to NECB are emissions to or uptake from the atmosphere of CO₂ (NEE), methane (CH₄), carbon monoxide (CO), and volatile organic C (VOCs); lateral or leaching fluxes of dissolved organic and inorganic C (DOC and DIC, respectively); and lateral or vertical movement of particulate carbon (nongaseous, nondissolved) by processes such as animal movement, soot emission during fires, water and wind deposition and erosion, and anthropogenic transport or harvest. Fluxes contributing to NEP are gross primary production (GPP), autotrophic respiration (AR), and heterotrophic respiration (HR).

Fig. 2. The relationship of carbon (C) fluxes to current measurement approaches. The background landscape image represents daily average GPP in Montana, USA, computed from MODIS satellite estimates of intercepted photosynthetically active radiation data at 250m spatial resolution. The figure also shows some of the vertical and horizontal carbon fluxes that add complexity (and are not incorporated) in this satellite-based C-flux estimate, including erosion, inputs and export of carbon as CH₄, CO and VOC, and lateral flow of respired CO₂ downslope, all factors that can confound measurements, depending on the scale. A floating aquatic chamber captures aquatic NEE; this (with a negative sign) is equivalent to NEP (=GPP – ER) plus CO₂ derived from terrestrial DIC that entered the lake in groundwater. A soil chamber captures belowground components of terrestrial heterotrophic and autotrophic respiration. An eddy

covariance tower captures the vertical component of terrestrial NEE; this (with a negative sign) is equivalent to NEP, when corrected for canopy storage, the advective flow of CO₂ from the forest to the valley, and leaching loss of respiration-derived DIC to the lake. The boundary-layer C budget, measured by aircraft and computed from differences in upwind and downwind CO₂ inventories, provides a sample of landscape-integrated (terrestrial and aquatic) NEE; it is also affected by remote sources, local disturbance fluxes and urban pollution; if lateral fluxes of DIC are small, NEE (with a negative sign) closely approximates NEP. NECB can be estimated from sequential measurements of ecosystem C stocks over time, but these changes are often too small to be detected except in very homogeneous ecosystems that are rapidly gaining or losing C. Measured fluxes can be compared with model inversions that calculate NECB at large scales (equivalent to NBP) from the geographic patterns of net CO₂ sources or sinks that would be required to produce observed patterns of atmospheric CO₂ transport. Since there is rarely a one-to-one correspondence between measurement techniques and conceptual fluxes, precision is required in defining both the conceptual fluxes and what is being measured as a function of method and scale.

Fig. 1

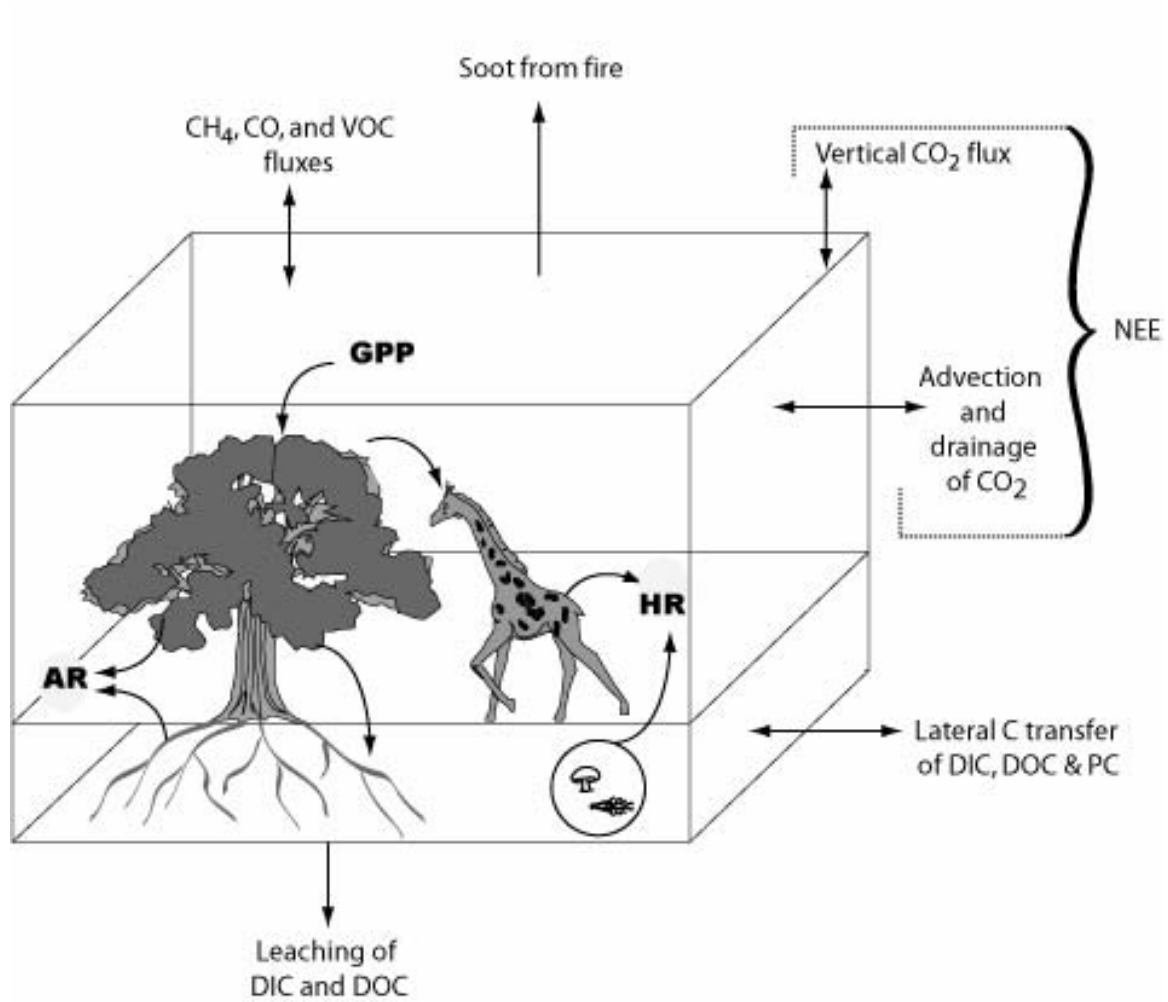


Fig. 2

