

Reconciling Carbon-Cycle Concepts, Terminology, and Methodology

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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 quantities 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 organic C accumulation in (or loss from) ecosystems. NECB differs from NEP when C fluxes other than C fixation and respiration occur. These fluxes include leaching; lateral transfer of organic C; emission of volatile organic C, methane, and carbon monoxide; and 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 (Wigley et al. 1996; Cox et al. 2000; Prentice et al. 2001; Fung et al. In press). As part of the 1997 Kyoto Protocol to the United Nations Framework Convention on Climate Change, countries may use increases in C storage by forests as one way to meet mandated reductions in C emissions from the burning of 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. Up to the present, the term that defines the sign and magnitude of this exchange—net ecosystem production (NEP)—has been used to represent two different quantities in the C-cycling literature (Lovett et al. In press). In this paper, we propose a clarification in the interest of avoiding further miscommunication and confusion.

An explosion of new methods available to study the C cycle, including geophysical techniques for flux estimation, isotopic techniques, and genomic approaches, has enabled scientists to quantify C fluxes or combinations of C fluxes that were not represented explicitly in the original conceptualization of the ecosystem C cycle. Atmospheric scientists and geophysicists have tended to focus on documenting C fluxes between ecosystems and the free atmosphere, whereas ecologists have traditionally focused on processes that transfer C between inorganic and organic forms (e.g., photosynthesis and respiration) or among ecosystem components (e.g., litterfall and consumption). While both groups (geophysical and ecological) have used similar terminology, the subset of fluxes captured by tower- to global-scale CO₂ flux estimates can be quite different from the subset addressed in ecological process studies.

Therefore, a second goal of this paper is to integrate these two C-cycling approaches, using a common conceptual framework and terminology. Finally we briefly describe how other C-cycling concepts relate to this common conceptual framework, with the goal of clarifying their definitions and pointing out ambiguities that require further research. Although complete consensus is unlikely, broad agreement on C cycling concepts and terminology among experts from diverse disciplines should improve communication about the central features of the C cycle.

Comparison of Geophysical and Ecological C Cycling Concepts

Geophysicists treat an 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. The net rate of C accumulation in the ecosystem equals the total input minus the total output from the ecosystem over a specified time interval. Different types of ecosystems may be dominated by radically different fluxes. In the short term, net ecosystem exchange (NEE; the net CO₂ exchange with the free atmosphere, i.e., the CO₂ flux across the upper surface and sides of the defined volume) is the largest flux in many terrestrial ecosystems. However, substantial C may be gained or lost by other pathways, such as leaching of dissolved organic C (DOC); emission of methane (CH₄), carbon monoxide (CO), and volatile organic C (VOC) compounds; erosion; fire; harvest; and other vertical and lateral transfers (Schlesinger 1997; Stallard 1998; Guenther 2002; Randerson et al. 2002). In streams, rivers, and estuaries, lateral C transfers

among ecosystems often dominate net C accumulation (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 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).

The ecological concept of C cycling addresses the biologically mediated C transfers that occur within the defined volume of the ecosystem (and not necessarily across its boundaries; Fig. 1). Carbon enters the organic component of the ecosystem as gross primary production (GPP; ecosystem-scale C fixation by all autotrophic C-fixing tissues) and is lost by respiration of autotrophs (autotrophic respiration, AR) and of heterotrophs (heterotrophic respiration, HR) such as animals and non-photosynthetic microbes. GPP is a flux across a very amorphous boundary defined by the leaf or cell surfaces, not the flux across the upper surface of the ecosystem volume. Some of the CO₂ fixed in GPP originated outside the ecosystem, and some is recycled from respiration within the defined volume. Ecosystem respiration losses act similarly; some of the respired CO₂ is exported from the ecosystem (as CO₂ or DIC), and some is recaptured by GPP.

The geophysical and ecological approaches to C cycling are complementary, one emphasizing the net C balance and the other the processes that regulate that balance. However, the two approaches can be integrated only if the fluxes being compared are carefully specified. Failure to specify component fluxes has been an important source of confusion about C cycling concepts.

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 (GPP) and ecosystem (plant, animal, and microbial) respiratory loss of CO₂-C (ER) and (2) as net rate of organic 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 GPP exceeds ER ($GPP/ER > 1$ (autotrophic ecosystems) or lose C when $GPP/ER < 1$ (heterotrophic ecosystems). In other ecosystems, such as streams, lateral flows of C and energy can dominate 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 storage of C in soils in chronosequences ≥ 1000 years is only about 0.3% of NPP, indicating that various respiratory processes and other loss pathways are quite efficient at burning up organic C (Schlesinger 1990). A similar quantity of C (0.3% of NPP) is transported from land to oceans by rivers, leaving the land in steady state over long time intervals (Schlesinger and Melack 1981). 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 (Fig. 1). 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 the term is not used consistently in the literature and that aquatic and terrestrial scientists differ in their prevailing definition of the term. In general, aquatic and atmospheric scientists have defined NEP as $GPP - ER$, whereas terrestrial scientists 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 common 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 suggest that Net Ecosystem Carbon Balance (NECB) be the term applied to the net rate of organic C accumulation in (or loss from) ecosystems. NECB represents the overall ecosystem balance of organic C from all sources and sinks—physical, biological, and anthropogenic. We recommend this term because it clearly designates a flux and not a stock of C.

The net flux of C into or out of an ecosystem (NECB) includes inorganic C fluxes that contribute to or derive from organic C plus inputs and outputs of organic C:

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

or

$$\text{NECB} = \text{NEP} + \text{import} - \text{export} - \text{nonbiological oxidations} \quad (2)$$

(Lovett et al. In press), where import and export refer to vertical and lateral fluxes of organic C and their non-CO₂ biological products (e.g., CO and CH₄), and nonbiological oxidations include fire in terrestrial ecosystems and oxidation of organic compounds by UV radiation in aquatic ecosystems. The major fluxes contributing to NECB are:

$$\text{NECB} = \text{NEP} - F_{\text{CO}} - F_{\text{CH}_4} - F_{\text{VOC}} - F_{\text{leach}} - F_{\text{fire}} - F_{\text{lat}} \pm F_{\text{other}} \quad (3)$$

where F_{CO} is CO efflux; F_{CH_4} is CH₄ emission (or CH₄ consumption; positive sign); F_{VOC} is VOC emission (or absorption; positive sign); F_{leach} is leaching loss of organic C; F_{fire} is C loss by

combustion and particulate emissions (or C input via smoke/ash deposition from regional fires; positive sign); F_{lat} is the lateral transfer of organic C out of (or into; positive sign) the ecosystem by processes such as animal movement, water and wind deposition and erosion, and anthropogenic transport or harvest; and F_{other} represents other fluxes that are normally small or unrecognized. Extrapolation of NECB to larger spatial scales has been termed net biome productivity (NBP) (Schulze and Heimann 1998). Fluxes other than NEP may be important in specific instances. In wetlands, for example, CH_4 emissions may be 10-20% of soil C emissions, and over long time scales C transfers associated with erosion, fire, and harvest may be of greater magnitude than NEP in determining NECB (Randerson et al. 2002).

It should be noted that NEP includes both atmospheric fluxes and leaching or lateral flow of DIC derived from respiration. These two types of fluxes require quite different measurement approaches and are seldom measured in the same study. Any estimate of NEP from field observations should therefore specify explicitly which fluxes are included in the NEP estimate and which fluxes are unmeasured or assumed to be negligible.

NECB can be measured directly in terrestrial ecosystems, particularly over long time scales, as the change in organic C stock 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), but in most other ecosystems C stocks change too slowly to be detected easily, given the substantial spatial variability in stocks. 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 (3% of NPP) (Andrews and Schlesinger 2001). These inorganic C accumulation rates are not captured in NECB (net change in organic C) but are typically small.

In contrast to terrestrial systems, NEP is often measured directly in aquatic systems. Since $NEP = GPP - ER$ can be measured in either C or oxygen currency, aquatic ecologists often use dissolved oxygen and sometimes oxygen isotopes to measure NEP (Hanson et al. 2003). The triple oxygen isotope method has also been used to measure NEP for the biosphere as a whole (Luz et al. 1999).

The key C fluxes (e.g., GPP, ER, NPP, NEP, and NECB) should have the same units (e.g., $\text{kg C ha}^{-1} \text{ yr}^{-1}$) and be independent of temporal and spatial scale, so estimates can be readily compared across scales. However, the fluxes that dominate C budgets and the techniques used to estimate them are quite scale-dependent. NBP explicitly includes infrequent events such as disturbance and therefore is most applicable at large temporal and spatial scales. Net ecosystem exchange (NEE) is the net inorganic C (CO_2) flux between the ecosystem and the free atmosphere. NEE has been used as a short-term (daily to annual) approximation of NEP (Baldocchi 2003). Aside from conventionally being opposite in sign (a positive NEE is a positive flux to the atmosphere), NEE differs from NEP ($= GPP - ER$) in omitting non-atmospheric gains and losses of inorganic C, such as the leaching loss from terrestrial ecosystems of dissolved inorganic C (DIC) derived from respiration, which has been estimated as 20% of NEP in arctic terrestrial ecosystems (Kling et al. 1991). In aquatic ecosystems NEE would also include atmospheric exchanges of CO_2 governed by physical processes, such as CO_2 solution or evasion in surface waters. NEE closely matches field estimates of C accumulation rate in some ecosystems; in other cases, particularly over long time intervals, other fluxes in equation 3 that are not included in NEE can comprise a significant proportion of ecosystem C exchange (Aumont et al. 2001; Richey et al. 2002; Folberth et al. 2005; Suntharalingam et al. In Press). Specifically,

$$NEE = F_{\text{evas}} - NEP - F_{\text{DIC}} \quad (4)$$

where F_{evas} is the physically controlled evasion of CO_2 (or dissolution; negative sign) and F_{DIC} is the leaching or lateral export of DIC (or import; positive sign).

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 complicate the use and interpretation of these terms.

Gross primary production (GPP) is the sum of gross C fixation by autotrophic C-fixing tissues at the ecosystem level (i.e., per unit ground 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).

GPP is often estimated in terrestrial ecosystems by incorporating eddy covariance measurements into a simple model that adds a temperature-corrected ecosystem respiration rate measured in the dark to net ecosystem C exchange (NEE) measured in the light (Falge et al. 2002). Two assumptions central to this approach in terrestrial ecosystems are (1) that leaching losses of DIC are negligible, as discussed earlier, and (2) that both foliar respiration and the temperature response of ecosystem respiration during the day are the same as at night. The validity of the second assumption is unclear, 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 the use of the respired CO₂ in photosynthesis (Loreto et al. 1999; Loreto et al. 2001). Alternatively, GPP can be estimated by summing NPP and autotrophic respiration measurements (Möller et al. 1954) or with models. GPP in aquatic ecosystems can be measured by diel changes in dissolved oxygen or CO₂ (although there is seldom a constant or 1:1 relationship between the two) or by changes in the gases in bottles in the light and in the dark (Howarth and Michaels 2000). Although this approach assumes that respiration measured at night or in dark bottles is the same as in the light, recent evidence indicates that respiration in the light can be substantially greater (Roberts et al. In press).

Autotrophic respiration (AR) is the sum of respiration rates (CO₂ production) of all living plant parts at the ecosystem level. 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 with other heterotrophs is conceptually cleaner but

their impact on plant nutrition and C balance and 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 at the ecosystem level.

Ecosystem respiration (ER) is the respiration of plants, animals, and microbes summed at the ecosystem level.

Net ecosystem production (NEP) is GPP minus ER.

Net ecosystem exchange (NEE) 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 biosphere may not reach the eddy flux 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 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 and in omitting non-atmospheric gains and losses of respiration-derived DIC (Fig. 1). NEE approaches NEP ($= GPP - ER$), when this latter flux is small.

Net primary production (NPP) is $GPP - AR$. NPP includes not only plant growth (biomass accumulation and tissue turnover above and below ground) but also the C transfer to herbivores and root symbionts (nodules, mycorrhizal fungi), 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).

Net ecosystem carbon balance (NECB) is the net rate of organic C accumulation in (or loss from) an ecosystem, regardless of the temporal and spatial scale at which it is estimated.

Net biome production (NBP) is NECB estimated at large temporal and spatial scales. The concept was developed to account for many of the fluxes unmeasured by NEE and explicitly includes disturbances that remove C from the system via non-respiratory processes such as fire 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:

$$NBP = \frac{\int_A \int_T NECB(x,t) dx dt}{T \cdot A} \quad (5)$$

where A is the land surface area considered, T is the temporal extent of the integration, and x,t are the spatial and temporal coordinates. Since 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 methodologies incorporate some, but not all of the fluxes we would like to document. 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 low 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). Janssens et al (2003), for example, showed that respiration of imported agricultural products had to be accounted for to interpret Europe's C budget correctly from atmospheric data. Most C cycle research gives insufficient attention to C fluxes associated with transported particulate and dissolved transported C, VOC and methane emissions, disturbance, harvest, and trade. The variable relationships among C cycling rates, oxygen transfers, and energy flow are often overlooked.

We need not only clear definitions of the conceptual components of C exchange but also clear terms for the fluxes that we can measure, and we must understand the relationship among these frequently divergent ways of viewing the carbon system. Until concepts are more clearly aligned with measurements, we risk serious misunderstanding or miscommunication about the role of human activities in the biosphere, making it difficult to apply our scientific understanding to the practical management of C emissions and sequestration.

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Figure legends

Fig. 1. Relationship among carbon (C) fluxes that determine NECB (all C imports to and exports from the ecosystem) and fluxes (in bold) that determine NEP (GPP, AR, and HR). The box represents the ecosystem.

Figure 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 volatile organic compounds, 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

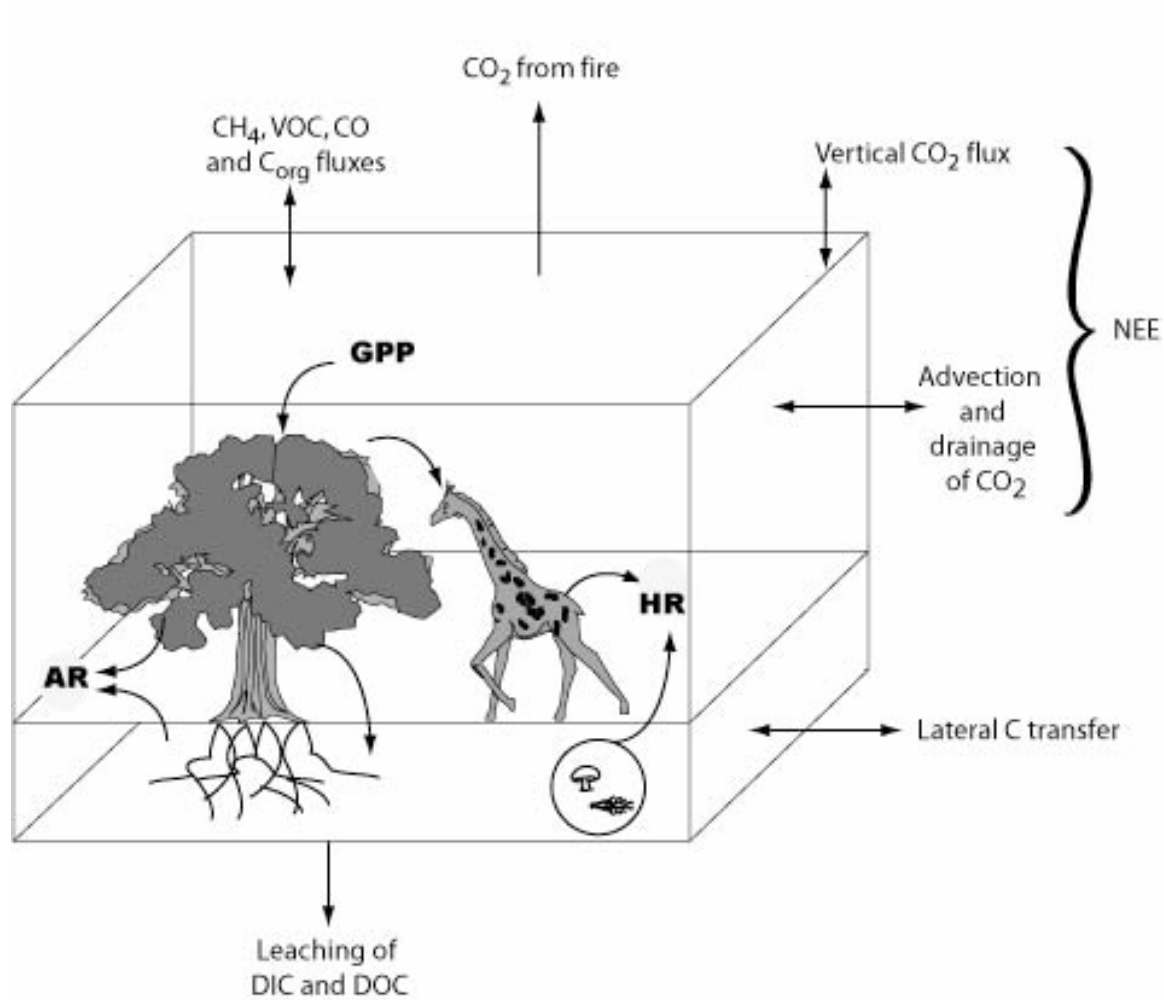


Fig. 2

