

NET ECOSYSTEM PRODUCTION: A COMPREHENSIVE MEASURE OF NET CARBON ACCUMULATION BY ECOSYSTEMS

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Abstract. The conceptual framework used by ecologists and biogeochemists must allow for accurate and clearly defined comparisons of carbon fluxes made with disparate techniques across a spectrum of temporal and spatial scales. Consistent with usage over the past four decades, we define “net ecosystem production” (NEP) as the net carbon accumulation by ecosystems. Past use of this term has been ambiguous, because it has been used conceptually as a measure of carbon accumulation by ecosystems, but it has often been calculated considering only the balance between gross primary production (GPP) and ecosystem respiration. This calculation ignores other carbon fluxes from ecosystems (e.g., leaching of dissolved carbon and losses associated with disturbance). To avoid conceptual ambiguities, we argue that NEP be defined, as in the past, as the net carbon accumulation by ecosystems and that it explicitly incorporate all the carbon fluxes from an ecosystem, including autotrophic respiration, heterotrophic respiration, losses associated with disturbance, dissolved and particulate carbon losses, volatile organic compound emissions, and lateral transfers among ecosystems. Net biome productivity (NBP), which has been proposed to account for carbon loss during episodic disturbance, is equivalent to NEP at regional or global scales. The multi-scale conceptual framework we describe provides continuity between flux measurements made at the scale of soil profiles and chambers, forest inventories, eddy covariance towers, aircraft, and inversions of remote atmospheric flask samples, allowing a direct comparison of NEP estimates made at all temporal and spatial scales.

Key words: atmospheric CO₂; biosphere–atmosphere fluxes; carbon accumulation by ecosystems; measuring; carbon balance; disturbance; net biome production; net ecosystem production; net primary production; scaling.

INTRODUCTION

Some of the biogeochemical processes that affect the carbon balance of terrestrial ecosystems include photosynthesis (Farquhar et al. 1980, Collatz et al. 1991), plant respiration (Ryan 1991), microbial respiration (Parton et al. 1993), leaching losses (Neff and Asner 2001), erosion (Stallard 1998), herbivory (McNaughton et al. 1989), fire (Crutzen and Andreae 1990), ice-sheet expansion and retreat (Harden et al. 1992, Schlesinger 1997), and rates of rock weathering (Berner 1993). Human appropriation and modification of the earth's surface over the last several centuries has altered many of these processes, with consequences for net ecosystem carbon fluxes, atmospheric mass balance, and inputs to oceans (Vitousek et al. 1986, Houghton 1996, DeFries et al. 1999). With attention focused by the Kyoto Protocol (Schulze et al. 2000) and subsequent international dialogue on carbon emissions from individual nations, there has been an in-

creasing need to define carbon budgets at regional and continental scales (Steffen et al. 1998). Unfortunately, direct measurements of carbon fluxes at regional to global scales are difficult with current technology (Tans 1993) so estimates of regional- and continental-scale C fluxes require the integration of remote atmosphere and satellite observations with field measurements and experimental manipulations (Running et al. 1999).

Initial investigations of biosphere–atmosphere carbon exchange made the assumption that the net flux can be approximated as the balance between photosynthesis and respiration (Keeling 1961, Machta 1972, Pearman and Hyson 1980, Fung et al. 1983). This was sensible given that many diurnal and seasonal patterns of atmospheric CO₂ concentration can be explained by considering only these two processes (Denning et al. 1996, Heimann et al. 1998). However, analysis of interannual and decadal dynamics in atmospheric CO₂ driven by changes within the terrestrial biosphere requires consideration of additional processes including fire, dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) losses in rivers, erosion, and land-use changes such as agriculture and timber harvest (Canadell et al. 2000, Pacala et al. 2001).

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TABLE 1. Summary of contemporary terrestrial ecosystem carbon fluxes.

Concept	Acronym/ symbol	Global flux	Definition
Gross primary production	GPP	~100–150 Pg C/yr	carbon uptake by plants during photosynthesis
Autotrophic respiration	R_a	~½ of GPP	respiratory loss (CO ₂) by plants for construction, maintenance, or ion uptake
Net primary production	NPP	~½ of GPP	GPP – R_a
Heterotrophic respiration (on land)	R_h	~82–95% of NPP	respiratory loss (CO ₂) by the heterotrophic community (herbivores, microbes, etc.)
Ecosystem respiration	R_e	~91–97% of GPP	$R_a + R_h$
Non-CO ₂ losses		~2.8–4.9 Pg C/yr	CO, CH ₄ , isoprene, dissolved inorganic and organic carbon, erosion, etc.; see Table 2.
Non-respiratory CO ₂ losses (fire)		~1.6–4.2 Pg C/yr	combustion flux of CO ₂ ; see Table 2.
Net ecosystem production	NEP	~±2.0 Pg C/yr	total carbon accumulation within the ecosystem; defined in <i>Defining Net Ecosystem Production: A comprehensive definition of NEP</i> .

In part because of the rapid expansion of carbon cycle analyses at regional to global scales, we are left with ambiguities in our conceptual framework (see Table 1 for a summary of ecosystem flux concepts). Should net ecosystem production (NEP), which was initially approximated in the first biosphere-atmosphere CO₂ studies as the difference between photosynthesis and respiration, formally include all carbon exchanges that influence net carbon accumulation by an ecosystem (as the name “net ecosystem production” implies)? Alternatively, should NEP refer solely to the photosynthesis and respiration components (as suggested by some recent analyses, e.g., Schulze and Heimann [1998], Steffen et al. [1998], and Buchmann and Schulze and [1999])?

DEFINING NET ECOSYSTEM PRODUCTION

Historical perspective

The simultaneous definition of NEP as the carbon accumulation within ecosystems and as the difference between gross primary production (GPP) and ecosystem respiration extends back in the ecological literature over four decades (Woodwell and Whittaker 1968, Woodwell and Botkin 1970, Reichle et al. 1975). These two definitions are equivalent when non-photosynthetic gains and non-respiratory losses to an ecosystem are negligible, and so in many applications over the last few decades the two definitions have been used interchangeably. Increasing interest in the global carbon budget and the partitioning of land and ocean carbon sinks in the late 1970s focused attention on the need to quantify non-respiratory losses from terrestrial ecosystems, including fire and river fluxes (Bolin et al. 1979). As described by Lugo and Brown (1986), even if the terrestrial biosphere were close to steady-state carbon balance, a substantial biosphere-atmosphere CO₂ sink would be required to match river carbon losses.

With new assessments of volatile organic compound (VOC), methane, fire, and river fluxes, the sum of non-CO₂ and non-respiratory losses from terrestrial ecosystems is substantial at stand, regional, and global scales. Combined, these fluxes represent a loss of ~10% of global net primary production (NPP) (Table 2), and thus provide motivation for defining NEP solely in terms of carbon accumulation at all scales of inquiry.

A comprehensive definition of NEP

To reconcile carbon flux measurements made with diverse techniques and across widely varying time and space scales, NEP must be defined as the rate at which carbon (C) accumulates within an ecosystem (i.e., the change in carbon storage over some time interval):

$$NEP = dC/dt. \quad (1)$$

A critical element of this definition is that the ecosystem in consideration must have defined boundaries in three dimensions (it must be possible to enclose the ecosystem with a three-dimensional container or box). For example, in a forest ecosystem, the top of the box might be defined as the height of the tallest tree, while the bottom of the box might be defined as a specified soil depth. Another critical feature of this definition is that the start and end times of the measurement period (or interval of integration) must be specified. Conservation of mass requires that fluxes (F) across the ecosystem boundaries equal the rate of change in C within the ecosystem. Thus, NEP has the equivalent definition (Olson 1963):

$$\begin{aligned}
 NEP &= F_{in} + F_{out} \\
 &\approx F_{GPP} + F_{R_e} + F_{fire} + F_{leaching} + F_{erosion} \\
 &\quad + F_{hydrocarbons} + F_{herbivory} + F_{harvest} + \dots \quad (2)
 \end{aligned}$$

Therefore, NEP encompasses all fluxes (F_i) across all the boundaries of the ecosystem, independent of the

TABLE 2. Global non-CO₂ and non-respiratory carbon losses from terrestrial ecosystems.

Source	Components	Flux (Pg C/yr)	Flux range (Pg C/yr)	Reference
Non-CO₂ losses				
Rivers	dissolved organic carbon	0.40	0.20–0.90	Schlesinger and Melack (1981), Degens (1982), Degens et al. (1991), Meybeck (1982), Suchet and Probst (1995), Stallard (1998)
	dissolved inorganic carbon	0.30	†	
Volatile organic compounds, VOCs	particulate organic carbon	0.30	†	Guenther et al. (1995)
	isoprene	0.50	†	
	monoterpene	0.12	†	
	other reactive VOCs	0.26	†	
	other non-reactive VOCs	0.26	†	
Methane	natural sources	0.16	0.11–0.21	Prather et al. (1996)
	anthropogenic biosphere	0.27	0.20–0.35	
Carbon monoxide, CO	fires	1.0	0.50–1.50	Bergamaschi et al. (2000)
	photochemical oxidation of organic matter	0.06	0.03–0.09	
	thermal oxidation of organic matter	0.04	0.01–0.08	Schade et al. (1999)
Non-respiratory CO₂ losses				
Fires	...	3.0	1.6–4.2	Crutzen and Andreae (1990)
Total sum of non-CO ₂ and non- respiratory CO ₂ losses‡	...	6.6	4.4–9.2	

† Range of estimates not available.

‡ Total flux is ~11% of global NPP at 60 Pg C/yr, which is ~6 times larger than the net terrestrial carbon flux estimated by Prentice et al. (2001).

driving mechanism or the degree of biological regulation (Fig. 1). This definition must include all fluxes because, in many instances, it is difficult to distinguish between C fluxes that are regulated solely by abiotic or biotic processes. Clear examples of fluxes with direct biological regulation include gross primary production

(GPP) and ecosystem respiration (R_e ; including both autotrophic and heterotrophic components) in which CO₂ diffuses directly through a cell membrane. Fluxes associated with fire (F_{fire}) and soil erosion ($F_{erosion}$) also are strongly regulated by biological and ecological processes, though not necessarily at a cellular level. The

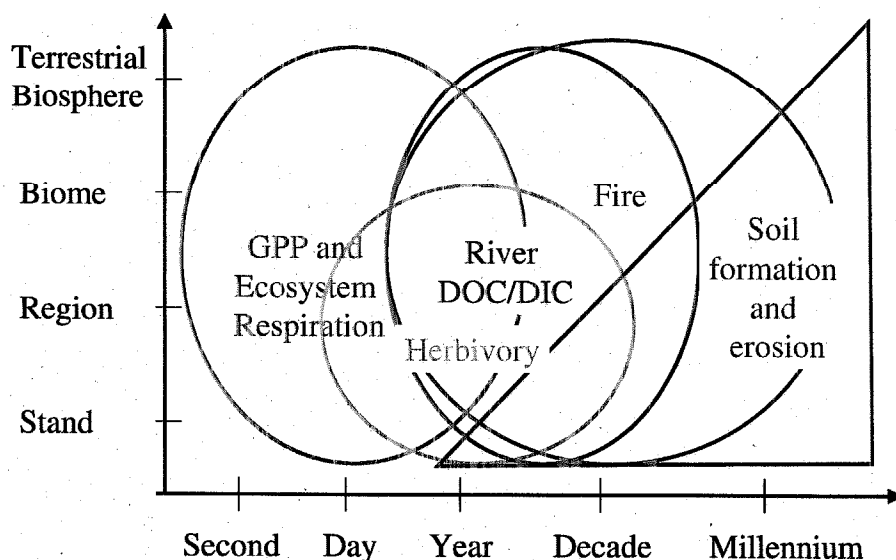


FIG. 1. Regulation of net ecosystem production (NEP) by processes in terrestrial ecosystems varies with the time-space scales. At longer timescales and larger spatial scales, dissolved organic and inorganic river fluxes (DOC/DIC), fires, and erosion play critical roles in regulating ecosystem carbon balance. On shorter timescales, gross primary production (GPP) and ecosystem respiration (R_e) are dominant processes.

fire flux (F_{fire} ; which includes CO_2 , CO , CH_4 , VOCs, and particulates) needs to be included in this definition, so that NEP is equivalent to the ecosystem mass rate of change over any timescale.

The role of non- CO_2 fluxes

Not all ecosystem C fluxes are in the form of CO_2 gas. Leaching (F_{leaching}) and hydrocarbon emissions ($F_{\text{hydrocarbons}}$) contribute significantly to NEP in many ecosystems. For example, in boreal peatlands and arctic tundra, vertical and lateral fluxes of dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), and methane are as much as 5% to 10% of the net ecosystem-atmosphere CO_2 flux (Waddington and Roulet 1997, King et al. 1998, Reeburgh et al. 1998). In tundra ecosystems, the inclusion of dissolved CO_2 and methane fluxes in calculations of NEP reduced carbon uptake rates by 20% relative to the ecosystem-atmosphere CO_2 flux (Kling et al. 1992). Isoprene, terpene, and other volatile organic compound (VOC) emissions also contribute to NEP (Lerdau 1991, Monson et al. 1991, Guenther et al. 1995).

While stream fluxes of DOC are generally within the range of 0–10 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ and average $\sim 5 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, there is large variability (2–52 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) across ecosystems (Hope et al. 1994). Rates of DOC flux are also substantially higher in soils than in streams, indicating the need to explicitly define a vertical (depth) ecosystem boundary in NEP calculations (Neff and Asner 2001). The impact of soluble carbon fluxes on carbon balance may be especially important in streams draining boreal forests and in areas with substantial wetland cover (e.g., Moore 1989, Hope et al. 1994, Waddington and Roulet 1997). Particulate C losses can also be substantial in some ecosystems, particularly following disturbance (Bormann et al. 1974, Stallard et al. 1998). Are these losses significant when integrated to the global scale? A 1 Pg C/yr net terrestrial flux evenly distributed over all biomes corresponds to approximately a 10 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ flux. Thus, when integrated, stream and river losses are comparable in magnitude to the net terrestrial flux (Prentice et al. 2001).

Carbon can also be removed or delivered to an ecosystem by lateral transfer of organic material, as mediated by herbivores ($F_{\text{herbivory}}$) (McNaughton et al. 1989) or harvest (F_{harvest}) (Harmon et al. 1990). In many cases herbivores are an internal component of an ecosystem, and will not cause a net transfer of C across the three-dimensional shape defined for the purpose of the NEP measurement. In other cases, herbivores may transfer C across the predefined spatial boundaries of the ecosystem, and thus contribute to NEP. Possible situations where this might occur include mass migrations, insect outbreaks, or agricultural grazing, or in any situation where the defined ecosystem is small as compared to the size of a typical herbivore. These components have not been explicitly incorporated into pre-

vious definitions of NEP although they have been frequently inferred as a part of heterotrophic respiration (Parton et al. 1993). Either we need still another concept that reflects total ecosystem C accumulation or (as we argue here) we need to explicitly include all C exchanges in NEP, so that this term truly reflects the net C accumulation by ecosystems, as has been implied in the past.

Disturbance and NEP

All of the flux components that contribute to NEP defined in Eq. 2 are either a direct result of disturbance events or are responding to a complex history of multiple disturbances that leave a long-term biological legacy (Reichle et al. 1975).

"Disturbance" is frequently defined as a relatively discrete event that induces widespread mortality of the dominant species within an ecosystem (e.g., Aber and Melillo 1991). Climate variability, N deposition, and stimulation of plant growth by elevated levels of atmospheric CO_2 are often considered as separate processes (in terms consequences for C fluxes), though they also have the potential to cause stand-leveling mortality events (Neilson 1993) and thus also have the potential to serve as agents of disturbance.

As with the definition of NEP described above, a comprehensive definition of disturbance should be based on clearly defined spatial boundaries and time intervals. Here we suggest following the framework developed by Pickett et al. (1989). Pickett et al. (1989) define the ecological concept of disturbance as a change in the minimal structure of a system caused by an external agent. Applying these concepts at the ecosystem scale, minimal structure includes the species composition, the distribution of plant functional types, and canopy architecture. Stand-leveling wind storms, fires, mortality induced by insect outbreaks, stand-killing droughts, and harvesting by humans all fundamentally alter this minimal structure and originate from a different level of ecological organization, thus qualifying as external agents. At the biome scale, a change in the disturbance regime from climate change or humans may constitute an external agent, with the ensemble of vegetation types and stand ages defining the minimum structure.

Human impacts on NEP

Humans affect all of the NEP components on the right-hand side of Eq. 2 by modifying the atmospheric composition, nutrient levels, climate, erosion rates, and disturbance regime. Examples of fluxes associated with humans include the removal of crops in agricultural ecosystems for use in distant feedlots and cities, the lateral transfer of wood from forests to paper mills, from paper mills to suburban and urban areas, and then to landfills, and the altered heterotrophic respiration of plowed soils when disturbance reduces the protection

of soil organic carbon from microbial attack (Kurz et al. 1995, Barlaz 1998, Skog and Nicholson 1998).

The dominant components of NEP vary with scale

As indicated in the discussion above, NEP potentially involves different processes and forms of carbon (i.e., not just CO_2). These processes are best represented and studied at certain scales. For example, disturbances such as fire kill individual plants and consume individual detritus parts, but are best considered in the NEP context at the level of landscapes or at the stand scale over very long time periods relative to the disturbance return interval. This is in part because the probability of a fire occurring increases with the extent of the temporal or spatial scale. At finer scales fires are irregular and they appear to add an unreasonable and often misleading variance in NEP. We suggest that this feature of NEP could be addressed by explicitly defining the level that NEP is being reported by use of subscripts. This would then clarify the processes that are usually included and excluded from the analysis. Any scaling of NEP from one level to another would then involve the addition of the processes that are most appropriately studied at that scale. For example, NEP at the level of individual stands ($\text{NEP}_{\text{stand}}$, with length scales roughly from 1 m to 1 km) would require study of fluxes associated with GPP (F_{GPP}), ecosystem respiration (F_{Re}), hydrocarbons ($F_{\text{hydrocarbons}}$), leaching (F_{leaching}), and erosion (F_{erosion}), although over short time spans the latter three terms might be neglected for some purposes. Fluxes associated with fire (F_{fire}), herbivory ($F_{\text{herbivory}}$), and harvest (F_{harvest}) may not be explicitly addressed at this scale (unless a disturbance occurs during a sampling interval). They would be seen at this scale as rare events that export C from the system. At larger scales, however, some of these processes would be seen as internal transfers while others would emerge as substantial contributors to NEP (Fig. 1).

Regional-scale estimates of NEP (NEP_{reg} , with length scales roughly from 1 km to 10^2 km) would include fluxes from a mosaic of stands with different disturbance histories and intensities. At this level, NEP is strongly regulated by direct CO_2 losses from fire and other disturbances as well as fluxes associated with GPP and R_e at various times following disturbance. It would include CO_2 emissions from crop burning, CO_2 and organics that enter groundwater and are subsequently emitted from lakes and streams, and CO_2 emitted from landfills and feedlots that was derived from NPP transported laterally from other ecosystems.

For the case of biome-level NEP ($\text{NEP}_{\text{biome}}$, with length scales roughly from 10^2 km to 10^4 km), fires, deforestation, erosion, and river DOC are significant contributing processes, even on relatively short time scales (months to years). At this scale, the impact of any individual disturbance event may be small compared with the ensemble of disturbance events that are simultaneously occurring, and human- and climate-in-

duced changes in the disturbance regime become critical regulators of NEP (Schulze and Heimann 1998, Canadell et al. 2000).

At the global scale, the integral of NEP over the entire land surface ($\text{NEP}_{\text{global}}$) represents the change in the total mass balance of the terrestrial biosphere, including plants, soils, herbivores, etc. NEP at this scale represents a transfer of C to ocean, atmosphere, and lithosphere reservoirs. By definition all transfers are internal, except the net flow to the atmosphere, oceans, or lithosphere. At the global scale, a clear definition of the borders of the terrestrial system is difficult given the dynamic mixing processes and CO_2 fluxes that occur at coastal margins and in estuaries.

The minimal scale for NEP

Use of a multiscale definition of NEP raises the issue of whether there is a minimal scale that emerges from NEP as a property. We suggest that this minimum scale is the same as the minimum scale for the definition of an ecosystem (Odum 1959). While most ecosystems include some combination of heterotrophs and autotrophs, the temporary or permanent absence of light-harvesting (photosynthetic) organisms clearly does not preclude application of the ecosystem concept neither should it preclude characterization of the ecosystem carbon balance with NEP.

MEASUREMENTS OF NEP AND BIOSPHERE-
ATMOSPHERE CO_2 EXCHANGE

On short timescales (typically less than a decade), it is difficult to accurately measure changes in total ecosystem carbon storage against large and heterogeneous stocks of C in soils and vegetation using Eq. 1. More precision can be obtained by measuring fluxes across the boundaries of the ecosystem via Eq. 2 (Fig. 2). Use of Eq. 2 to estimate NEP requires that we identify and measure the dominant components of the flux. In practice, it also requires the conscious decision to neglect certain components, if they are believed to be small at the temporal or spatial scale of measurement.

At the time and space scale of eddy covariance flux measurements, the dominant one-way components of NEP are GPP and R_e . This has led to the definition of net ecosystem exchange (NEE) as the balance between GPP and R_e at half-hour to decadal time intervals (Wofsy et al. 1993). Defined in this way, NEE is a partial flux out the top of a three-dimensional box enclosing the ecosystem and is equivalent to NEP (Eq. 1 and 2) only at sites where other lateral and vertical C fluxes are demonstrably small. NEP at eddy flux tower sites in managed forests also includes any lateral removal of coarse woody debris in the footprint area, in addition to the ecosystem-atmosphere CO_2 flux. A tower in an eroding field might record a net uptake of C, even though NEP is at steady state, with ecosystem-atmosphere gains balanced by erosion losses (Harden et al. 1999). Moreover, the ecosystem boundaries should be

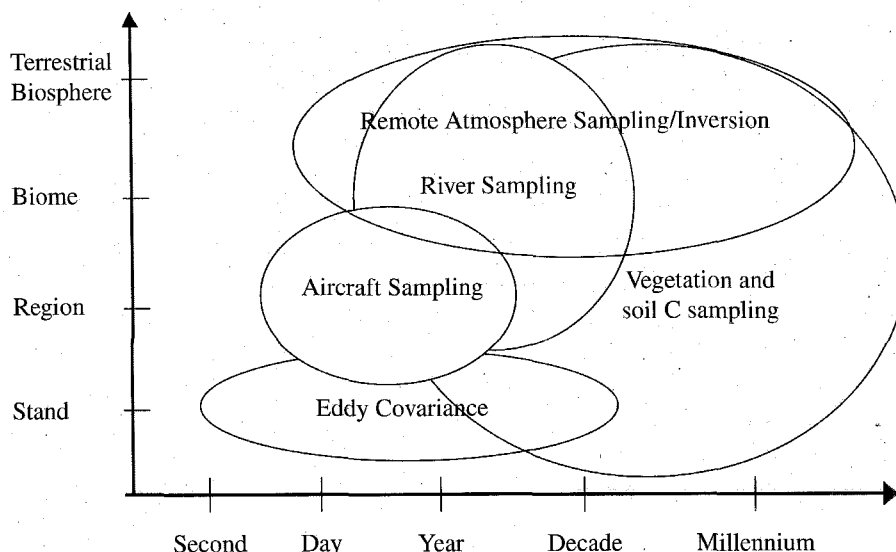


FIG. 2. The temporal and spatial domain of different techniques used to measure components of net ecosystem production (NEP) in terrestrial ecosystems. Atmospheric-inversion methods have been applied to contemporary flask CO_2 measurements as well as ice-core records extending over the last 1000 years (Joos et al. 1999, Rayner et al. 1999). Eddy covariance flux measurements from the Harvard Forest (Petersham, Massachusetts, USA) extend over one decade (Wofsy et al. 1993).

clearly defined in stand- and regional-scale flux studies by disturbance age, erosion setting, and other key variables that affect NEP as it is "scaled up" to regional or global estimates (e.g., Rapalee et al. 1998).

For similar reasons, biosphere-atmosphere CO_2 fluxes inferred from atmospheric model inversions of CO_2 flask or aircraft measurements (Rayner et al. 1999) are also only partially representative of terrestrial NEP. At the global scale, river runoff contains DOC (dissolved organic C) and DIC (dissolved inorganic C) of mixed terrestrial and aquatic origin on the order of 0.2–0.9 Pg C/yr for DOC and 0.3 Pg C/yr for DIC (Schlesinger and Melack 1981, Degens 1982, Meybeck 1982, Degens et al. 1991, Suchet and Probst 1995). As previously stated, if the terrestrial biosphere were at steady state, then this net hydrologic C transport would require a one-way atmosphere-biosphere flux of the same magnitude (Lugo and Brown 1986). Estimates of C accumulation within the terrestrial biosphere based on atmosphere-biosphere fluxes must account for these hydrologic losses, and also assess the spatial domain and timescale over which the land-ocean flux returns to the atmosphere in coastal margins and in the open ocean. Atmospheric inversions of CO_2 will also fail to properly assign sources and sinks of total C when oxidation of CH_4 , CO, and some VOCs occur in atmospheric regions that are offset from their terrestrial sources.

On timescales greater than a decade, it is possible to measure changes in total ecosystem C storage (Fig. 2). Chronosequences of stands of different ages show decade-to-century scale increases in C stocks following clearing (Richter et al. 1999), glacial retreat (Crocker and Major 1955, Harden et al. 1992), floodplain development (Yarie et al. 1998), fire (Harden et al. 2000),

and large C losses associated with disturbance (Kasichke et al. 1995, Cohen et al. 1996). The C accumulation over any long time period depends on GPP (gross primary production) and the respiration of newly fixed carbon, respiration and other loss pathways for carbon that was fixed prior to the last disturbance, and carbon losses associated with the disturbance event. For example, NEP measurement following disturbance includes variable proportions of recent and old soil C (Trumbore and Harden 1997, Goulden et al. 1998).

NEP AND NET BIOME PRODUCTION

The new concept proposed by Schulze and Heimann (1998)

To address the issue of disturbance (which was widely neglected in initial biosphere-atmosphere modeling analyses and field measurement programs), Schulze and Heimann (1998) proposed the concept of net biome production (NBP), defined as the regional net carbon accumulation after considering C losses from fire, harvest, and other episodic disturbances. Specifically, the NBP concept acknowledges that small but consistent rates of C accumulation over most of the land surface (i.e., what occurs in most forests and grasslands) must be balanced by relatively infrequent, but large-magnitude releases associated with episodic disturbance (e.g., Rapalee et al. 1998). The infrequent nature of these release events makes it difficult to design terrestrial sampling programs that provide a true measure of the regional- or continental-scale C flux (Schulze and Heimann 1998).

In the definition of NBP, Schulze and Heimann (1998) distinguish between directional forcing (such as

changing levels of atmospheric CO_2 or temperature) and disturbance by episodic forcing (such as fires and harvest). According to Schulze and Heimann (1998), directional forcing affects NEP (net ecosystem production) fluxes through changes in NPP and microbial and herbivore respiration. In contrast, episodic disturbance is said to only affect NBP because of the different time scale and impact on ecosystem processes (frequently decimating aboveground and belowground biomass stocks) and the different measurement approach required. NBP is considered as a downstream flux at the landscape, regional, or continental scale, after stand-level fluxes of GPP, R_a , R_h , and NEP have been estimated. Here we question whether episodic disturbances that are included in NBP can be partitioned conceptually or practically from processes that are included in NEP.

Ambiguities introduced by the NBP concept

The distinction between NEP and NBP has limitations that compromise communication among biogeochemists, atmospheric scientists, and ecologists working at different scales. The limitations stem from three sources: (1) The definition of NBP assumes episodic disturbance and directional forcing can be distinguished from one another, allowing an unambiguous partitioning of fluxes between NEP and NBP. (2) The definition of NBP suggests that other terrestrial C fluxes (GPP, NPP, R_a , and NEP; Table 1) can be estimated (either measured or modeled) separately from episodic disturbance (and thus NBP). (3) The name and definition of NBP implies that episodic disturbance emerges only as a regulator of C fluxes at continental or "biome" scales, as a downstream process from NEP. We address these issues in the following paragraphs.

In many instances, episodic disturbances and directional forcing cannot be easily separated, yet our framework (and carbon accounting systems) must be rigorous enough to include this reality. For example, temperature increases could be classified as a directional forcing (and thus fall under NEP in the definition proposed by Schulze and Heimann [1998]). Consider the case, however, of a severe temperature or drought event that kills some of the vegetation. How much of this mortality must occur before the flux is considered NBP instead of NEP? If fire is an annual occurrence, as in many grassland ecosystems, or consumes only a small fraction of the vegetation, as in many ground fires, is this an episodic disturbance? Similar issues arise with herbivory and wind damage. Low levels of insect herbivory and wind damage are common in most ecosystems, while outbreaks and hurricanes may be relatively infrequent. If an outbreak or windstorm does occur, at what level of severity does it constitute an episodic disturbance vs. a directional one? Low levels of herbivory are usually treated as a component of NPP, but if certain levels of herbivory are counted in NBP one needs to decide which form goes with which process.

In the case of harvest, ecosystems may experience severe disturbance of the soil and canopy understory during clearing (Black and Harden 1995) or harvest may be restricted to removal of berries or removal of dead wood for fuel (Hao and Liu 1994). Should the harvest flux (associated with NBP according to Schulze and Heimann [1998]) include the changes in soil respiration triggered by harvest removal or subsequent soil erosion?

The implications of attempting to separate episodic and directional forcing are severe. Previous estimates of global NEP based on the assumption that episodic disturbances are associated only with the NBP flux, are as high as 10 Pg C/yr into the land surface (Steffen et al. 1998, Prentice et al. 2001). Yet, as shown in the examples above, it is unclear as to exactly what fluxes should be included when NEP is defined in this way. It is essential that we separate our theoretical paradigm of terrestrial C balance from our ability (or inability) to accurately measure the net flux and its components. From a practical perspective, NEP and NBP are impossible to measure separately (it is impossible to make a pure measurement of NEP following the NBP-NEP distinction presented in Schulze and Heimann [1998], Buchmann and Schulze [1999], and Schulze et al. [2000]).

Disturbance is an integral and defining element of all ecosystems. Therefore measurements of GPP, NPP, R_a , and R_h are impossible to consider outside the context of both episodic disturbance and directional forcing. For example, canopy photosynthetic capacity depends strongly on leaf nitrogen, which in turn, depends on soil N availability and the cumulative history of disturbance events that have precipitated N loss (Field and Mooney 1986, Schulze et al. 1994). Likewise, ecosystem respiration fluxes critically depend on total ecosystem carbon stocks and their distribution among live, labile, chemically recalcitrant, and physically protected forms (Schimel et al. 1994). Again, past disturbance frequencies and intensities are critical regulators of the distribution and amounts of C in these forms. The definition of NBP does not emphasize the fundamental role of episodic disturbance in shaping "upstream" fluxes (GPP, NPP, R_a , and R_h); the primary effect of disturbance is assumed to occur at very large spatial scales (Buchmann and Schulze 1999: Fig. 1).

Within every square meter of an ecosystem, the net C balance (and all of the one-way components) is influenced by the cumulative history of multiple, previous disturbances. In the boreal forest, for example, logs remain after fire from trees that grew two or more fire cycles previously and are still decomposing. Harden et al. (2000) found that it was very difficult to distinguish between heterotrophic respiration from the decomposition of organic material exposed or killed during the last major disturbance and microbial respiration of decomposing leaf and root litter derived from living vegetation.

Reconciling NBP with NEP

Because of the ambiguities created by distinguishing between NBP and NEP, we suggest a conceptual framework where NBP is equivalent to a comprehensive definition of NEP (see *Defining NEP: A comprehensive definition*, above) at regional or global scales. Thus, NBP also represents the total mass balance of terrestrial C:

$$\text{NBP} = \text{NEP} = dC/dt. \quad (3)$$

Is the concept of "net biome productivity" then necessary? Given the conceptual framework described by ecologists over the last few decades (Woodwell and Whittaker 1968, Reichle et al. 1975, Lugo and Brown 1986, Aber and Melillo 1991), NBP does not represent a quantity that is fundamentally different from NEP. However, the NBP concept is extremely useful because it highlights the role of rapid episodic fluxes in shaping NEP at very large scales and the challenges of extrapolating terrestrial C measurements made at individual sites (where these rapid episodic fluxes are not easily measured). NBP also highlights the non-negligible contribution of lateral (harvest) fluxes out of ecosystems that may be very difficult to quantify at individual sites.

While there is value in the NBP concept, we believe that it is impossible to attempt to partition fluxes from the terrestrial biosphere in terms of their origin as either arising solely from episodic disturbance or directional forcing from climate or other processes, or to make a unique distinction between NEP and NBP.

NEP, NBP, AND CARBON MANAGEMENT

The relevance of disturbance effects on carbon exchange is also important to the development of C emission restrictions in the Kyoto Protocol.⁷ Article 3.4 of the protocol includes the possibility that ecosystem-management activities focused on containing disturbances such as fire and pest outbreaks could be considered for carbon uptake credits. At the scale of countries or continents, disturbance-associated C fluxes are very large. For example, the direct loss of C during boreal forest fires is predicted to reach as high as 0.8 Pg C/yr over the next 30–100 yr (Kasischke et al. 1995). Reductions in the rates of these emissions could, in theory, qualify for C credits. The amount of C that could be affected by such policy decisions is significant. For example it has been suggested that a 5% reduction in fire-induced C losses in United States could yield a 0.5 Pg C/yr reduction in C emissions (Sohngen and Haynes 1997).

The critical issues involving NEP (net ecosystem production) and NBP (net biome production) estimates from a policy perspective are based on the need to document changes in C storage associated with management activities. For the reasons discussed in this

manuscript, it is critical to clearly define the boundaries of the region considered for C balance and to evaluate the impacts of previous disturbances on current rates of C uptake or loss at all spatial and temporal scales. Without consideration of these two issues, the accounting requirements defined in the Kyoto Protocol for the inclusion of terrestrial C fluxes in a broader C restriction cannot be met.

CONCLUSIONS

1) A robust definition of net ecosystem production (NEP) should be based on a full ecosystem mass balance and include non-CO₂ and non-respiratory components of the C flux and clearly defined temporal and spatial boundaries. Defined in this way, NEP provides an unambiguous measure of change in C storage that is conceptually consistent across all spatial and temporal scales, from an individual plot to the entire terrestrial biosphere. In our view, definitions of NEP solely based on the difference between NPP and R_h or GPP and R_a encourages a perspective in which other C transfers are ignored at the local scale, and thus reconciling carbon mass balance with ocean and atmosphere reservoirs becomes difficult at the global scale.

2) Disturbance is an integral property of all ecosystems. It affects all one-way C fluxes including GPP, R_a , and R_h , and hydrologic fluxes at all spatial and temporal scales. It does not emerge as a regulator solely at regional or biome scales.

3) Net biome production (NBP) as previously defined by Schulze and Heimann (1998) cannot be distinguished from NEP in many instances because episodic disturbance is frequently impossible to distinguish from directional forcing and because most C fluxes respond to disturbance over a wide range of temporal scales.

4) Equivalent mass-balance definitions of the two terms "NBP" and "NEP" allows for a consistent treatment of carbon in political frameworks for taxation, and for efficient comparison of fluxes at various spatial and temporal scales and between models and field observations.

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⁷ URL: <http://www.unfccc.de/resource/convkp.html>

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