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COMMENTARY

Is Net Ecosystem Production Equal to Ecosystem Carbon Accumulation?

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ABSTRACT

Net ecosystem production (NEP), defined as the difference between gross primary production and total ecosystem respiration, represents the total amount of organic carbon in an ecosystem available for storage, export as organic carbon, or nonbiological oxidation to carbon dioxide through fire or ultraviolet oxidation. In some of the recent literature, especially that on terrestrial ecosystems, NEP has been redefined as the rate of organic carbon accumulation in the system. Here we argue that retaining the original definition maintains the conceptual coherence between NEP and net primary production and that it is congruous with the widely accepted definitions of ecosystem autotrophy and heterotrophy. Careful evaluation of NEP highlights the various potential fates of nonrespired carbon in an ecosystem.

Key words: net ecosystem production; carbon accumulation; net primary production; gross primary production; total ecosystem respiration.

INTRODUCTION

Net ecosystem production (NEP) is a fundamental property of ecosystems. It was originally defined by Woodwell and Whittaker (1968) as the difference between the amount of organic carbon (C) fixed by photosynthesis in an ecosystem (gross primary production, or GPP) and total ecosystem respiration R_e (the sum of autotrophic and heterotrophic respiration). Defined this way, NEP represents organic C available for storage within the system or loss from it by export or nonbiological oxidation. The sign of NEP defines whether an ecosystem is autotrophic (NEP greater than zero, as in a typical forest or grassland) or heterotrophic (NEP less than zero, as in cities and many lakes and rivers). The original definition of NEP as the difference between GPP and R_e is conceptually parallel to the definition of net primary production (NPP), which is the difference between GPP and autotrophic respiration (Woodwell and Whittaker 1968). The reporting of NEP for various ecosystems has increased in recent years as ecosystem scientists investigate more fully the controls on the C balance of the biosphere. However, terrestrial ecosystem studies often estimate NEP as the rate of C accumulation, (for example; Lichter 1998; Caspersen and others 2000; Wirth and others 2002), and a recent paper and even a widely read textbook explicitly equate NEP with C accumulation rate (Randerson and others 2002; Chapin and others 2002). The goal of this essay is to explain why, in our view, this is incorrect.

NEP can best be understood within the context of a complete organic C balance for an ecosystem, which can be written as:

$$\Delta C_{org} = GPP + I - Re - E - Ox_{nb} \qquad (1)$$

where GPP and R_e are as defined above, ΔC_{org} is the change in organic C storage in the ecosystem, I is the import of organic C, E is the export of organic C, and Ox_{nb} is nonbiological oxidation of C, for

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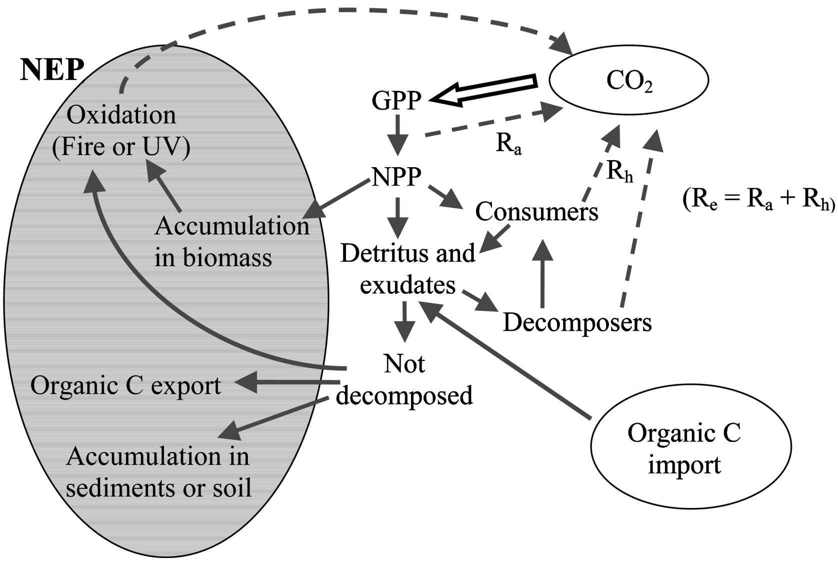

Figure 1. Fates of organic carbon (C) fixed in or imported into an ecosystem. Total ecosystem respiration (R_e) is the sum of autotrophic respiration (R_a) and heterotrophic respiration (R_h). The *shaded area* contains the components of the NEP of the system. ''*Accumulation in biomass*'' represents all biomass (plant, animal, or microbial); the *arrow* is drawn from NPP in this diagram because plant biomass accumulation is generally the largest biomass term. NPP, net primary production; NEP, net ecosystem production; GPP, gross primary production; CO_2, carbon dioxide; UV, ultraviolet.

instance by fire or ultraviolet (UV) oxidation. This equation requires one to specify the boundaries of the ecosystem and a specific time interval over which the change in C storage is evaluated. The terms in Eq. 1 are usually expressed as mass of C per unit area for that specified time interval, or sometimes as instantaneous rates (i.e., mass area^{-1} time^{-1}).

If NEP is defined as:

$$\mathrm{NEP} = \mathrm{GPP} - \mathrm{R_e} \tag{2}$$

then

$$\mathrm{NEP} = \Delta \mathrm{C}_{org} + \mathrm{E} + \mathrm{Ox_{nb}} - \mathrm{I} \tag{3}$$

and

$$\mathrm{NEP} + \mathrm{I} = \Delta \mathrm{C}_{org} + \mathrm{E} + \mathrm{Ox_{nb}} \tag{4}$$

In aquatic ecosystems, NEP is usually measured directly from the mass balance of oxygen (O_2) or carbon dioxide (CO_2) (for example, Cole and others 2000; Hanson and others 2003). Total respiration is obtained from the gas balance at night (when GPP is zero) and then GPP is calculated from Eq. 2. This gas balance approach is also the basis for estimating NEP in some terrestrial systems using eddy covariance techniques, or globally using large-scale atmospheric data with some additional isotopic measurements (for example, Luz and others 1999). In terrestrial studies, however, NEP is often calculated by summing the fates of NEP in the ecosystem, usually just using the ΔC_{org} term and ignoring the other terms on the right-hand side of Eq. 3.

Equation 4 and Figure 1 illustrate the potential fates of NEP, plus any organic C imported into the system, as either (a) storage in the ecosystem, for instance as an increment of the organic C pool in vegetation, soils, or sediments; or (b) export from the ecosystem, for instance as dissolved organic C, particulate C, or as harvest removal of organic material; or (c) nonbiological oxidation by fire or UV oxidation. Thus, NEP represents the C potentially available for storage within a system, but not all of the NEP is necessarily stored. Similarly, some C that is stored within an ecosystem may have been imported into the ecosystem rather than fixed there, and would not contribute to the system's NEP.

A few simple examples will help to clarify these points. First, consider a forest ecosystem, with the lower bound of the ecosystem set at the bottom of the rooting zone. If some of the C that is fixed by photosynthesis in the forest leaches below the rooting zone as dissolved organic carbon (DOC), that C is not stored in the ecosystem but represents part of the NEP because it is fixed by the autotrophs but not respired within the ecosystem. Likewise, if this forest grows for 50 years and then is harvested, with some of the woody material removed from the ecosystem, the C in the harvested wood should be included in the calculation of NEP even though it was exported from the system. This is exactly parallel to the fact that herbivory and detrital losses are included in the calculation of NPP.

A somewhat more problematic issue is the calculation of NEP if the forest were burned rather than harvested. Some of the C lost during the fire would be exported from the system as organic C in soot and smoke, and some of it would be nonbiologically oxidized to CO_2. Both of these losses should be included if NEP is calculated by summing its potential fates, as in Eq. 3. For example, if a forest accumulated 100 g C/m^2/y over 50 years, and in year 50 a fire consumed all of the accumulated 5,000 g C/m^2, the NEP over the 50-year period would still be 5,000 g C/m^2 even though there would be no C accumulation in the system. In this case, the fate of the NEP is in the export and nonbiological oxidation terms of Eq. 3.

Consider also a lake ecosystem surrounded by a forest. If leaves from the forest blow into the lake, then sink to the bottom of the lake and accumulate in the sediments, does this C storage increase the NEP of the lake? The answer is no, because the leaves contribute equally to the import (I) and C accumulation (ΔC_{org}) terms in Eq. 3, so the NEP is not affected. If the leaves were partially decomposed before storage in the sediments, the CO_2 loss would increase ecosystem respiration and thus cause the lake's NEP to be more negative. This type of C subsidy from terrestrial ecosystems is the reason that lakes can simultaneously have positive C accumulation and negative NEP.

Measuring NEP can be challenging, especially in terrestrial ecosystems. Estimates of terrestrial ecosystem production and respiration (if NEP is calculated from Eq. 2) and of soil and vegetation C accumulation (if NEP is calculated from Eq. 3) typically have high uncertainities. Some studies compare both methods of calculation (for example, Hamilton and others 2002). In recent years, eddy covariance techniques have been used frequently to estimate NEP. By measuring the vertical net flux of CO_2 above the ecosystem, eddy covariance measurements estimate the total CO_2 exchange, often called the ''net ecosystem exchange'' (NEE). Net ecosystem exchange is equal to the NEP plus sources and sinks for CO_2 that do not involve conversion to or from organic C (although the NEE is by convention opposite in sign, so that fluxes into the ecosystem are negative):

$$-\text{NEE} = \text{NEP} + \text{inorganic sinks for } CO_2 - \text{inorganic sources of } CO_2 \quad (5)$$

Examples of inorganic sources and sinks are weathering reactions, precipitation or dissolution of carbonates, and atmosphere–water equilibrations. Although they are likely to be minor terms in the CO_2 exchange of a forest (but see Raymond and Cole 2003), these inorganic sources and sinks can be very important in the ocean. The ocean has become a very large sink for atmospheric CO_2 in the industrial era, storing some 2 Gt C/y at present. This storage is almost entirely due to the diffusion of atmospheric CO_2 into sea water that in the preindustrial era, when CO_2 levels were lower, had been in equilibrium with the atmosphere. Biology is a very minor factor in this flux (for example, Siegenthaler and Sarmiento 1993; Broecker and others 1979).

Randerson and others (2002) suggest that the definition of NEP be changed to equate NEP with the rate of C accumulation in the ecosystem. They argue that we need a term for C accumulation, and that the term ''NEP'' should be appropriated for that use. We maintain that NEP has a different meaning, and that the change in the organic C pool per unit time should simply be called the organic carbon accumulation rate. It would be positive for an increment in C and negative for a decrement. Net ecosystem production is a useful term for a concept that is different from C accumulation – it is the amount of organic C fixed in an ecosystem that is not respired there and is therefore available for accumulation, export, or nonbiological oxidation. Net ecosystem production may be a good approximation of the organic C accumulation rate within the system if inputs and outputs of organic C are negligible, but it is incorrect to assume that NEP and organic C accumulation are always equivalent. Many studies in the literature have used NEP and organic C accumulation interchangeably, with the implicit assumption that import, export, and nonbiological oxidation of organic C are negligible. However, in many cases, these terms cannot be ignored. In fact, at continental to global spatial scales, the major fate of terrestrial NEP is export as riverine DOC (Schlesinger 1997).

Schulze and others (2000) proposed the term ''net biome production'' to integrate the terrestrial C balance over larger spatial and temporal scales, but we agree with Randerson and others (2002) view that net biome production is simply organic C accumulation at a larger scale and that it would be an unnecessary addition to an already confusing list of terms.

We recommend retaining the original definition of NEP as GPP minus R_e because (a) it represents a useful concept, (b) it is congruous with the accepted definition of autotrophic and heterotrophic systems, and (c) its similarity to NPP provides a cohesive set of conceptual constructs for ecosystem ecology. Net ecosystem production should not be equated with organic C accumulation in theory or in practice unless the other terms in Eq. 3 can be shown to be negligible.

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