

What is NPP? Inconsistent accounting of respiratory fluxes in the definition of net primary production

S. H. ROXBURGH,* † ‡ S. L. BERRY,* † ‡ T. N. BUCKLEY,* § B. BARNES* † ‡ and M. L. RODERICK* † ‡

*Cooperative Research Centre for Greenhouse Accounting, ‡Ecosystem Dynamics Group, §Environmental Biology Group, Research School of Biological Sciences, Institute of Advanced Studies, The Australian National University, Canberra ACT 0200, Australia

Introduction

Primary production represents a globally important flux of carbon between the atmosphere and the biosphere. From an ecological perspective, it measures the rate at which solar energy is stored by plants as organic matter, and is therefore a measure of the rate at which solar energy is captured and made available to the rest of the food chain (Odum 1971). From a biogeochemical perspective, primary production provides links between the biosphere and the climate system through the global cycling of C, water and nutrients (Roy *et al.* 2001).

Gross primary production (GPP) is the total amount of C assimilated by plants within a given area over a specified timeframe. (Here GPP refers to the total C fixed by photosynthesis, minus the C lost by photorespiration. We have adopted the convention of specifying productivity in units of C mass per unit ground area per unit time, although we could have alternatively used units of total biomass, or energy: Odum 1971.) Net primary production (NPP) is GPP less the flux of autotrophic respiration of assimilate used for the plant's own metabolism (*R*), therefore:

$$\text{NPP} = \text{GPP} - R \quad \text{eqn 1}$$

Despite its apparent simplicity, we show that equation 1 has been interpreted in at least two fundamentally different ways. In the first, NPP is constrained to have a minimum possible value of zero. In the second, NPP can take both positive and negative values.

The purpose of this note is to identify and provide an explanation for these differing interpretations, and to focus attention more generally on the potential ambiguities embedded within equation 1. We also briefly discuss the implications for the field measurement of primary production. Our hope is that, through a more detailed consideration of equation 1, we not only highlight current inconsistencies in its application, but also encourage future researchers to exercise care when defining and using NPP.

We begin by deriving equation 1 from first principles, to make explicit the various terms and their origin.

A general expression for the instantaneous rate of change of the total living biomass C stock (*C*) is given by:

$$\frac{dC}{dt} = \text{GPP}' - R' - L' \quad \text{eqn 2}$$

where GPP' is the instantaneous rate of gross photosynthesis, *R'* is the instantaneous autotrophic respiration rate, and *L'* is the total of all the instantaneous non-respiratory losses of C (e.g. litterfall, herbivory, root death, exudation, disturbance). As GPP', *R'* and *L'* all represent instantaneous rates, they can, and do, fluctuate markedly and asynchronously over time.

Because NPP is defined over a finite time interval (τ), integration of equation 2 is required:

$$\int_0^\tau \frac{dC}{dt} dt = \int_0^\tau (\text{GPP}' - R' - L') dt$$

$$C_\tau - C_0 = \int_0^\tau \text{GPP}' dt - \int_0^\tau R' dt - \int_0^\tau L' dt \quad \text{eqn 3}$$

$$= \tau \overline{\text{GPP}'} - \tau \overline{R'} - \tau \overline{L'}$$

Assuming the definition in equation 1, NPP over the interval τ is therefore:

$$\text{NPP} = \int_0^\tau \text{GPP}' dt - \int_0^\tau R' dt \quad \text{eqn 4}$$

or, alternatively:

$$\text{NPP} = \tau \overline{\text{GPP}'} - \tau \overline{R'} \quad \text{eqn 5}$$

In this formulation we have defined gross production, respiration, and hence net production, to be the sum of the fluxes over a given time interval (equation 4). Alternatively, the terms can be interpreted as average fluxes over the time interval, multiplied by that time interval (equation 5). The most appropriate interval for integration is often considered to be 1 year, although monthly intervals for integration are also common. In general, any value of τ can be validly chosen. However, the choice of τ has implications for interpretation of the calculated NPP. In particular, measurements made over a given period may not be representative of the longer-term flux. It is for this reason that sub-yearly

measurements, for example taken over a few consecutive weeks or months, should not, in general, be linearly scaled and expressed on a yearly basis.

Because the time interval is commonly taken to be a single month, season or year, $\tau = 1$ is often assumed and is therefore dropped from equation 5. It is also often implicitly assumed that the terms involving GPP' and R' represent the sums of these fluxes over the interval, and these symbols are also eliminated, yielding equation 1.

Having discussed the origins of equation 1, and the importance of the measurement period τ , in the remainder of this paper we discuss the different ways in which this equation has been interpreted, with particular emphasis on differences in the definition of the respiratory flux term R .

Interpretation 1: NPP must be ≥ 0

Under this interpretation, the minimum possible value of NPP is zero, reflecting the view that NPP is a measure of the increment of new organic material to the ecosystem from photosynthesis. For example Begon *et al.* (1986) state: 'The total fixation of energy by photosynthesis is referred to as *gross primary productivity* (GPP). A proportion of this is respired away by the plant itself and is lost from the community as respiratory heat (R). The difference between GPP and R is known as *net primary productivity* (NPP) and represents the actual rate of production of new biomass ...'. (Begon *et al.* 1986, p. 649).

A similar definition is given by Clark *et al.* (2001): 'NPP is defined as the total new organic matter produced during a specified interval' (Clark *et al.* 2001, p. 357).

A minimum NPP of zero is also consistent with a number of theoretical approaches, although it is unclear whether the assumptions underlying these methods constrain NPP to be positive, or whether NPP can conceptually be negative, but in the model representations the values are positive due to, for example, annual or longer integration periods. The widely used Miami model (Lieth 1975) predicts NPP from annual mean temperature and precipitation, with all possible predicted NPP values constrained to be ≥ 0 . Similarly, there are a number of plant production models where NPP is assumed to be a fraction of GPP, typically around 0.45 (Roxburgh *et al.* 2004).

Interpretation 2: NPP can be negative

The second interpretation allows NPP to be negative, and is most commonly encountered in the modelling literature, for example Kicklighter *et al.* (1999) state: '... the models that calculate NPP as the difference between gross primary productivity (GPP) and autotrophic respiration (R_A) can calculate a negative NPP in months when R_A is greater than GPP.' (Kicklighter *et al.* 1999, p. 21). This quote is from a review of 17

global estimates of NPP, where negative NPP was predicted by some of the models, mainly during the winter months (see Fig. 5 of Kicklighter *et al.* 1999). While data were not presented to explore these results in greater detail, the authors noted that 14 of the 17 models were at least capable of generating negative NPP estimates.

Although the time interval in the above example is 1 month, negative NPP has also been reported for annual integration intervals. In the study of six dynamic global vegetation models by Cramer *et al.* (2001), three of the models reported negative annual NPP, particularly in arid biomes. The three models were Hybrid (Friend *et al.* 1997), Ibis (Foley *et al.* 1996) and Triffid (Cox 2001). Simulations were run over a 339-year period commencing in 1861 and, depending on the particular year and model, annual NPP was estimated to be negative over an area ranging from 1 to 35% of the total global terrestrial surface, excluding Antarctica.

Finally, Adams *et al.* (2004) recently analysed 10 NPP-calculating algorithms and identified the parameter space within which these models estimate negative NPP, typically involving conditions of high temperature and low water availability.

How can these two interpretations be reconciled?

The observation that some NPP-calculating algorithms allow negative values and some do not has been noted in the literature (Kicklighter *et al.* 1999; Adams *et al.* 2004), but the potential for such discrepancies to reflect a deeper definitional problem than just imperfections underlying different modelling approaches has not been generally appreciated. In this section we revisit equation 1, taking a closer look at its underlying assumptions. We achieve this through a graphical analysis of the various components contributing to plant biomass accumulation and loss (Fig. 1).

In Fig. 1 the sizes of the shaded boxes represent C stocks at the beginning and end of a measurement year (boxes a and d), and also the fate of the C stocks during the year (boxes b and c). Following equation 2, we recognize respiratory (R) and non-respiratory losses (L) where these are each split into new (R_{new} , L_{new}) and old (R_{old} , L_{old}) components. The subscript 'old' refers to C that had been fixed prior to the measurement period.

Some of the C residing in living vegetation at the start of the year (box a) is lost during the year (box b). Here, R_{old} refers to autotrophic respiratory losses associated with the metabolism of stored C compounds, for example vegetative growth following disturbance, or the respiratory cost of initiating new-season growth in deciduous vegetation.

At the same time as C is lost from existing vegetation, new C is being accumulated by photosynthesis (box c). The total C fixation over the year is GPP, and some of this will be used during the year for the plants' own metabolism through autotrophic respiration (R_{new}). Similarly, some of this newly assimilated material is lost,

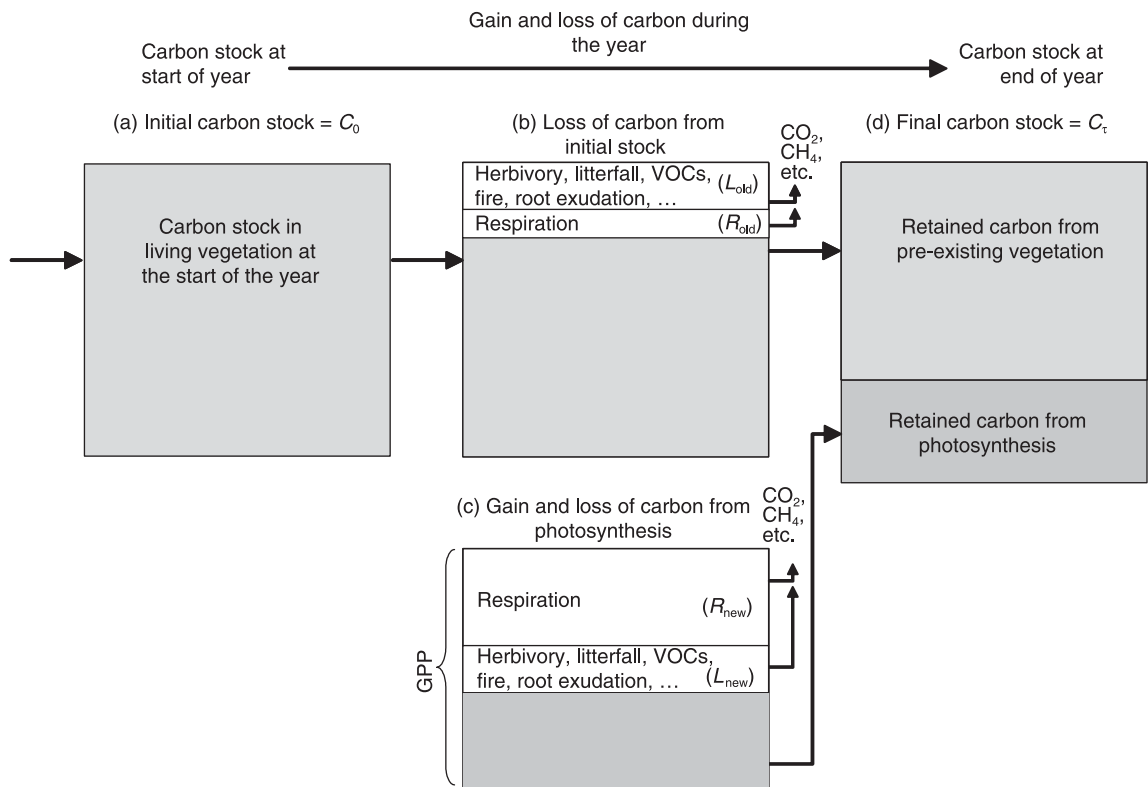


Fig. 1. Graphical representation of the accumulation and loss of C within a hypothetical ecosystem over the course of 1 year. The areas of the shaded boxes are proportional to the mass of the C stocks they represent.

for example through the rapid (within-year) turnover of leaves, fine-root turnover, root exudations, etc. (L_{new}).

At the end of the year, the total C stock (box d) is therefore a combination of that remaining from the initial stock (box d, light grey), and that remaining from the current year's photosynthesis (box d, dark grey). The net change in C mass during the year is the difference between the C stocks at the beginning of the year (box c) and the end (box d). This equates to the term $C_t - C_0$ in equation 3.

Separate identification of the four loss terms (L_{old} , L_{new} , R_{old} , R_{new}) provides the key to understanding the basis for the two different interpretations. In the first, where NPP is constrained to be ≥ 0 , the corresponding relationship is:

$$NPP_1 = GPP - R_{new} \quad \text{eqn 6}$$

In this case, $NPP_1 \geq 0$ because R_{new} is always $\leq GPP$.

In the second interpretation, where NPP can be negative, the representation is:

$$NPP_2 = GPP - (R_{new} + R_{old}) \quad \text{eqn 7}$$

Here, if conditions are such that the plants are metabolizing significant amounts of stored C from the products of previous years' photosynthesis, then it is possible for the combined autotrophic respiration term ($R_{new} + R_{old}$) to exceed GPP, and therefore for NPP_2 to be negative.

Although separating the respiratory and other losses from C fixation in the current and previous years is essential to understanding the different interpretations of NPP, only rarely have the terms of equation 1 been represented in this way. The study by Kira *et al.* (1967) provides the closest correspondence to our analysis, where losses due to litterfall and herbivory (but not respiration) were represented explicitly for growth in the current year *vs* previous years. Kirschbaum *et al.* (2001) and Ricklefs (1973) also discussed the potential importance of separating the current year's growth components from those of previous years.

It is worth emphasizing that the distinction between equations 6 and 7 and their underlying assumptions are independent of the integration period, τ (equation 5). As an example, consider the calculation of NPP over the course of a single day. On a day-to-day basis NPP_2 , as calculated by equation 7, will often be negative, for example when photosynthesis during the day is low, but where autotrophic respiration at night remains high. In contrast, NPP_1 over the same day calculated according to equation 6 will be positive, as R_{new} must always be $\leq GPP$ (Fig. 1). At the very extreme, if the integration interval is so short that no photosynthesis occurs, for example during the night, then $GPP = 0$, R_{new} must also be zero, and therefore NPP_1 is also zero. In contrast, NPP_2 will be either zero or negative, depending on the magnitude of the respiration of C fixed prior to the integration period (R_{old}).

We have attributed the difference in the two interpretations of NPP to differences in the accounting of the respiration of current *vs* previously fixed C (Fig. 1, equations 6 and 7). However, in modelling studies where negative NPP has been estimated, such partitioning of the respiration fluxes has never been made. Rather, negative NPP arises in these models when the gross production (GPP) and autotrophic respiration (R) fluxes are calculated independently, and when R is estimated to be $>GPP$. We note that, regardless of the method of calculation, if $R > GPP$, this must be because some of the C fixed prior to the measurement period has been respired.

While equations 6 and 7 clarify the conceptual basis of the different interpretations of NPP, in a practical sense there are formidable difficulties in separating, by field-based measurement, C loss and gain from current growth *vs* growth stored from previous periods. These are discussed below.

Implications for field measurement of NPP

The most common method for estimating NPP in terrestrial ecosystems is the harvest method, where the change in ecosystem biomass over the sampling period is added to estimates of the appropriate loss terms. Using the various components identified in Fig. 1, assuming equation 6 ($NPP \geq 0$), and with $\tau = 1$ implicitly assumed, then:

$$\begin{aligned} C_\tau - C_0 &= \text{total C gains} - \text{total C losses} \\ &= GPP - (R_{\text{new}} + R_{\text{old}} + L_{\text{new}} + L_{\text{old}}) \\ &= GPP - R_{\text{new}} - (L_{\text{old}} + R_{\text{old}} + L_{\text{new}}) \\ &= NPP_1 - (L_{\text{old}} + L_{\text{new}} + R_{\text{old}}) \quad \text{eqn 8} \\ NPP_1 &= (C_\tau - C_0) + (L_{\text{old}} + L_{\text{new}}) + R_{\text{old}} \end{aligned}$$

Net primary production as per the first definition is therefore estimated as the change in biomass over the measurement period ($C_\tau - C_0$), plus the total loss of C due to herbivory, litterfall, etc. ($L_{\text{old}} + L_{\text{new}}$), plus the loss of C resulting from the respiration of pre-existing material (R_{old}).

Assuming the second definition for NPP (equation 3), then the relationship is:

$$\begin{aligned} C_\tau - C_0 &= \text{total C gains} - \text{total C losses} \\ &= GPP - (R_{\text{new}} + R_{\text{old}} + L_{\text{new}} + L_{\text{old}}) \\ &= GPP - (R_{\text{new}} + R_{\text{old}}) - (L_{\text{old}} + L_{\text{new}}) \\ &= NPP_2 - (L_{\text{old}} + L_{\text{new}}) \quad \text{eqn 9} \\ NPP_2 &= (C_\tau - C_0) + (L_{\text{old}} + L_{\text{new}}) \end{aligned}$$

A number of consequences stem from a comparison of equations 8 and 9. First, if R_{old} can be assumed to be zero, then the two calculations are the same. Second, for both equations only *total* litterfall, herbivory and other non-respiratory losses ($L_{\text{old}} + L_{\text{new}} = L_{\text{total}}$) need be measured, without any requirement to separate material originating from current *vs* previous years' growth. This simplifies field measurement.

Appropriate methods for measuring the various losses of C contained within the sum L_{total} have been critical to estimation of NPP by the harvest method. The most commonly considered are litterfall losses and losses due to herbivory, although other fluxes, such as the release of volatile organic C compounds, fine-root turnover, and root exudations, are also well recognized (Clark *et al.* 2001; Scurlock *et al.* 2002). There are also difficulties in the measurement of total root growth, and in ensuring all components of the vegetation (e.g. grasses, shrubs and trees) are adequately represented in field sampling programmes. None of these quantities is easily measured, with the result that NPP is often underestimated. For example, Scurlock *et al.* (2002) concluded that harvest-based estimates of grassland NPP may be underestimated by as much as a factor of 2–5, and Robinson (2004) discusses the potential for global root biomass estimates to be as low as 60% of actual.

If the preferred definition is NPP_1 , with NPP constrained to be ≥ 0 , then the requirement to measure respiratory losses from pre-existing material (equation 8) clearly adds to these already formidable difficulties. Indeed, R_{old} would seem to be impossibly difficult to measure, as it would require first measuring autotrophic respiration, a difficult enough task on its own, and then partitioning this flux into the components originating from growth in the current and previous years. Because the potential importance of the term R_{old} has never been explicitly recognized, experimental estimates of NPP have therefore implicitly used equation 9, even though the aim may have been to measure only the net increment from 'new' photosynthesis (equation 8). As noted above, using equation 9 in this context is valid only if $R_{\text{old}} = 0$.

Concluding comments

Consistent and unambiguous definitions are a cornerstone of science, allowing researchers to communicate effectively, and results from various studies to be compared. It is therefore worrying to admit that we are still grappling to define primary production – one of the most fundamental and widely studied quantities of ecosystem function. In particular, we have shown that the origin of the fluxes that contribute to NPP are not satisfactorily discriminated, with the result that at least two fundamentally different conceptions of NPP are in current use.

In order to improve this situation, it is imperative that both empirical and theoretical researchers clarify through careful definition which components of NPP are being considered. We have shown that a key issue is the distinction between the respiration of C fixed during the measurement period, and the respiration of C that was assimilated in previous years.

The answer to the question 'can NPP be negative?', is clearly yes – depending on how it is defined. The question of whether NPP should be allowed to be negative is of greater interest, and raises the issue of what

it is we want NPP to measure. Quantifying the net fixation of energy by photosynthesis over the interval (equation 6) is ecologically appealing, and addresses directly the rate at which new resources are being added to the biosphere. In contrast, including total autotrophic respiratory losses in the definition (equation 7), thus allowing NPP to be negative, may be the most appropriate when viewed from a C-cycle/biogeochemical perspective. It also appears that this latter definition is the easiest to measure empirically, as it does not require estimation of the potentially troublesome term R_{old} . Whether scientists can agree on a standardized definition of NPP remains to be seen. At the very least, we urge that the distinction between the two alternative formulations needs to be made more clearly in both current and future NPP studies.

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