Net primary production of forests: a constant fraction of gross primary production?

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Summary Considerable progress has been made in our ability to model and measure annual gross primary production (GPP) by terrestrial vegetation. But challenges remain in estimating maintenance respiration (R_m) and net primary production (NPP). To search for possible common relationships, we assembled annual carbon budgets from six evergreen and one deciduous forest in Oregon, USA, three pine plantations in New South Wales, Australia, a deciduous forest in Massachusetts, USA, and a *Nothofagus* forest on the South Island of New Zealand. At all 12 sites, a standard procedure was followed to estimate annual NPP of foliage, branches, stems, and roots, the carbon expended in synthesis of these organs (R_g), their R_m, and that of previously produced foliage and sapwood in boles, branches, and large roots. In the survey, total NPP ranged from 120 to 1660 g C m^{-2} year^{-1}, whereas the calculated fraction allocated to roots varied from 0.22 to 0.63. Comparative analysis indicated that the total NPP/GPP ratio was conservative (0.47 ± 0.04 SD). This finding supports the possibility of greatly simplifying forest growth models. The constancy of the NPP/GPP ratio also provides an incentive to renew efforts to understand the environmental factors affecting partitioning of NPP above and belowground.

Keywords: forest growth models, forest productivity, growth respiration, maintenance respiration, NPP/GPP ratio.

Introduction

In recent years, our ability to calculate the amount of CO_2 assimilated by photosynthesis (gross primary production, GPP) has improved significantly as a result of the development of new experimental and modeling techniques. The eddy correlation method has allowed accurate measurement of ecosystem C fluxes over whole growing seasons at several sites (Baldocchi et al. 1996, Goulden et al. 1996) and there are now available detailed and validated models of radiation absorption and canopy photosynthesis such as MAESTRO (Wang and Jarvis 1990a, 1990b), BIOMASS (McMurtrie et al. 1990, 1994), BEX (Bonan 1991a, 1991b) and MBL/SPA (Williams et al. 1996). Although FOREST-BGC (Running and Coughlan 1988, Running and Gower 1991) and MBL/CSA (Williams

et al. 1997) are aimed at wider-scale simulations and treat radiation interception and canopy photosynthesis in less detail, these models still provide good estimates of GPP over longer intervals when compared against daily and monthly eddy flux data and annual whole-tree carbon balances (e.g., Waring et al. 1995, Williams et al. 1997). Landsberg and Gower (1996) have reviewed these models (except for MBL/SPA and MBL/CSA) and assessed their performance. They all recognize implicitly (or, in the case of BIOMASS, explicitly) that not all the photosynthetically active radiation absorbed by stands is effective in photosynthesis.

McMurtrie et al. (1994) proposed the term 'utilizable radiation' for the amount of photosynthetically active radiation that can be used by the canopy for photosynthesis. It is calculated by discounting the radiation absorbed by the canopy, determined by the ratio of average to maximum stomatal conductance, irrespective of whether reductions in conductance are caused by high vapor pressure deficits, low soil water content in the root zone, or subfreezing conditions. The procedure was described by Landsberg (1986) and has been applied by McMurtrie et al. 1994, Runyon et al. 1994, Waring et al. 1995 and Landsberg and Waring 1997.

Calculation of GPP is only the first step. The result required from stand growth models, either aimed at predicting forest productivity, or calculating carbon balances, is usually not GPP but net primary production (NPP). However, it has proved difficult to calculate NPP accurately from GPP because of the uncertainties associated with the estimation of respiration (see Equation 1, below). Developing their model of forest productivity, Landsberg and Waring (1997) circumvented the difficulties of calculating respiration by assuming that the NPP/GPP ratio is approximately constant, with a mean value of about 0.45 for temperate forests. This value was based on several sets of published and unpublished data. A similar approach to that of Landsberg and Waring (1997) has been applied by Gifford (1993, 1994) to an analysis of the global carbon balance based on extensive laboratory experiments. In this paper we describe and analyze in detail information that we have recently collected from additional field studies, to test the validity of this important assumption.

Estimation of NPP

Over any time interval Δt we define NPP as:

$$NPP = GPP - R, \tag{1}$$

where R includes stand growth and maintenance respiration. The difficulty in using Equation 1 as the basis for estimating NPP in the field lies in the uncertainties associated with the estimation of respiration. Work by Linder and Troeng (1981), Ryan (1991a), Ryan et al. (1995), and others, has led to considerable progress in this area, but the difficulties remain formidable. We must account for growth and maintenance respiration and the variations associated with the respiration of different tissues (leaves, the living tissue of stems, structural and fine roots), with the nitrogen content of tissues and with temperature.

An important finding is that stem biomass, although a major carbon store, generally requires less than 10% of annual gross primary production to maintain the small fraction of living cells associated with sapwood and phloem (Ryan 1991b, Ryan et al. 1995).

The time interval (Δt) may also be important, because values of the NPP/GPP ratio measured over periods of hours and days are unlikely to be the same as those obtained from measurements made over longer periods, particularly for forests with seasonally deciduous canopies. Over short periods, we would expect responses to be dominated by the biochemical processes involved in maintenance and ion exchange respiration, which are strongly affected by temperature, whereas over longer periods the influence of growth respiration, which is seasonally variable, may play a more dominant role on plant carbon balance. Furthermore, the apparent Q_{10} of the temperature response of respiration will be affected by the way temperature is measured and averaged in relation to respiration measurements.

Net primary production can also be estimated from information about biomass dynamics:

$$NPP = \Delta(\text{standing biomass}) + \text{losses}, \tag{2}$$

where the losses are from biomass produced during the interval Δt.

Measurements of aboveground standing biomass, and changes in it over time, are (at least in principle) relatively simple to make, as are measurements of litter fall. However, root production and turnover are notoriously difficult to measure directly. Estimates of coarse-root production are fairly conservative, and generally average < 20% of aboveground production for a wide range of species and coarse-root production is directly correlated with growth in stem diameter (Santantonio et al. 1977, Santantonio and Hermann 1985, Beets and Pollack 1987; $r^2 > 0.9$). But fine-root production and turnover are difficult to measure and the carbon costs associated with fine roots are highly variable, depending on factors such as soil type and fertility and water status (Beets and Whitehead 1996, Landsberg and Gower 1997, Landsberg and Waring 1997). Based on a compilation of world literature, Raich and Nadel-

hoffer (1989) established a relationship between the efflux of CO_2 from the soil and leaf litter fall that sets an upper limit to the amount of carbon allocated annually to roots. The procedure has been endorsed by Gower et al. (1996) for general estimates, although they warned that it may lead to serious errors when used to estimate the carbon allocated to roots in a single stand. Ryan (1991a) and Ryan and Waring (1992) used the relationship to estimate total allocation of carbon to roots in lodgepole pine and Pacific silver fir stands. In a later study, Ryan et al. (1996) modified the procedure to allow for separation of coarse root growth.

Data analysis

Table 1 contains information about the dominant species, site and stand characteristics in which the measurements of NPP and respiration that we have used were made. In all of the studies, aboveground net primary production of foliage, branches, and stems was obtained from locally determined allometric relationships with stem diameter at breast height (1.4 m). Measured increases in stem diameter over periods from 1 to 5 years permitted calculation of increments in all of the aboveground components. Growth respiration was considered to represent 25% of the carbon sequestered in the synthesis of aboveground biomass. Belowground net primary production by roots was not measured directly; instead a relationship based on litter fall (Raich and Nadelhoffer 1989) was used to estimate total belowground allocation (i.e., net production plus growth and maintenance respiration). We further assumed, as did Ryan (1991a), that 50% of the belowground allocation went to production with 25% to each of the respiration terms.

Ryan et al. (1995) prepared estimates of sapwood maintenance respiration at Site 3 (western hemlock, Douglas-fir) and showed that the annual value was around 7% of GPP. For the other sites across the Oregon transect, maintenance respiration (R_m) of stem and branch sapwood was estimated by assuming a similar ratio of maintenance respiration to aboveground production as was found at Site 3 (around 18.5%). Maintenance respiration of leaves was calculated according to the procedure outlined by Ryan (1991a, 1991b) and Ryan (1995), in a form that integrates daily and seasonal temperature amplitude, assuming a linear increase with the nitrogen content of live tissue, and an exponential response to temperature. For Stands 1–6 along the Oregon transect, the formula used to estimate foliage maintenance respiration was:

$$R_m = \sum_{d=1}^{d=365} \tau N_d R_0 \exp(\beta T_d) I_0(\beta A_d), \tag{3}$$

where R_m = annual maintenance respiration (g C m^{-2} year^{-1}), N_d = total canopy foliar or sapwood N content (g m^{-2} ground area), R_0 = respiration rate per g N at 0 °C (Ryan 1991a, 1991b, Ryan 1995), β = temperature response, 0.069 ($Q_{10} = 2.0$), A_d = daily temperature amplitude, $(T_{max} - T_{min})/2$, I_0 = a function to correct for diurnal variation in temperature (Ågren and

Table 1. Characteristics of the sites from which data were analyzed to provide annual carbon budgets.

Stand no.	Dominant species	Latitude and longitude	Elev. (m)	Annual precip. (mm)	Annual total PAR MJ m^{-2} year^{-1}	Mean annual temp. (°C)	Growing season (Julian days)	Max. LAI proj.	Canopy height (m)
1[1]	Picea sitchensis Tsuga heterophylla	45°03′ N 123°57′ W	240	2510	1934	10.1	75–320	6.4	50
1a[1]	Alnus rubra	45°03′ N 123°57′ W	200	2510	1934	10.1	110–275	4.3	13
2[1]	Pseudotsuga menziesii Quercus garryana	44°36′ N 123°16′ W	170	980	2267	11.2	75–280	5.3	40
3[1]	Tsuga heterophylla Pseudotsuga menziesii	44°40′ N 122°36′ W	800	1180	2259	10.6	75–305	8.6	30
4[1]	Tsuga mertensiana Abies lasiocarpa Picea engelmanii	44°25′ N 121°50′ W	1460	1810	2088	6.0	160–256	1.9	20
5[1]	Pinus ponderosa	44°25′ N 121°40′ W	1030	540	2735	7.4	125–275	0.9	7
6[1]	Juniperus occidentalis	44°17′ N 121°20′ W	930	220	2735	9.1	125–275	0.4	10
7a[2]	Pinus radiata (untreated control)	35°21′ S 148°56′ E	630	790	3030	13.3	1–365	3.1	21
7b[2]	Pinus radiata (irrigated)	35°21′ S 148°56′ E	630	790	3030	13.3	1–365	3.0	23
7c[2]	Pinus radiata (fertilized and irrigated)	35°21′ S 148°56′ E	630	790	3030	13.3	1–365	4.6	24
8[3]	Quercus rubra Acer rubrum	42°32′ N 72°11′ W	340	1100	2000	6.3	140–300	3.5	24
9[4]	Nothofagus truncata	41°31′ S 172°45′ E	600	1500	2790	10.7	1–365	7.4	21

[1] NPP Data from Runyon et al. (1994), components of respiration from Williams et al. (1997).

[2] Analysis presented by Ryan et al. (1996), but modified by assuming allocations belowground were 50% to NPP and 50% to respiration.

[3] NPP Data from Aber et al. (1993); additional information from Williams et al. (1997).

[4] Analysis presented by Benecke and Evans (1987), with respiration not identified as to type.

Axelsson 1980), τ = scales R_o to a daily rate, and T_d = mean daily temperature.

Additional details of the measurement methods and procedures used in the various studies can be obtained from the original publications.

Table 2 contains the NPP, respiration and GPP values obtained from the published studies, with units standardized. Radiation absorption/canopy photosynthesis models were used to estimate GPP in several of the studies cited, but the GPP values presented in Table 2 were all obtained by summing the reported NPP and respiration values, as indicated below the table. Note that GPP ranges from 302 to 3439 g C m^{-2} year^{-1}, with NPP ranging from 122 to 1661 g C m^{-2} year^{-1}. We checked the accuracy of our budget method with independent measurements of GPP made at Harvard Forest (42°32′ N, 72°11′ W) using eddy flux and chamber methods. Our budget estimate was 1246 g C m^{-2} year^{-1}, and the flux estimate of GPP from 4 years of non-drought conditions was 1190 g C m^{-2} year^{-1} (Goulden et al. 1996).

The NPP values in Table 2 are plotted against the GPP values in Figure 1, where a linear regression has been fitted to the data. The slope is 0.47 ± 0.04 (SD), which is not significantly different from the NPP/GPP ratio of 0.45 ± 0.05 used by Landsberg and Waring (1997).

Discussion

Although our comparisons are mainly for temperate and a few subalpine forests, the likelihood that the ratio of NPP/GPP is similar in other biomes is high, based on comparable results (slightly higher, but stable ratio of NPP/GGP) obtained in growth room studies with more than a half-dozen species exposed to a range of temperatures from 15 to 30 °C (Gifford 1994). The reason for this constant ratio may be tied to the C/N ratio in plants. Over the course of a year, for every mole of C gained by a forest, about 0.5 mole must be spent in metabolism. There are strong relationships between the N content of vegetation and rate of leaf photosynthesis, the fraction of NPP allocated to foliage, and maintenance respiration of living tissues. The constant ratio of annual respiration to annual gross photosynthesis for the broad range of stands examined indicates that the relationship between these processes is highly linear at this scale. In terms of climatic warming and rising CO_2 concentrations, many models assume that photosynthesis will not be able to match increases in autotrophic and heterotrophic respiration; however, the acceleration of decomposition should release additional nitrogen into the ecosystem and further stimulate canopy development and photosynthesis to the extent that there may be no net carbon lost to the

Table 2. Component carbon analyses for stands identified by number (Column 1) in Table 1. Data are presented separately for net primary production of all aboveground components (Column 2) and for roots (Column 7). Growth respiration is combined for all aboveground components (R_g). Maintenance respiration (R_m) was subdivided into leaves (Column 4), and stems and branches (Column 5). Estimates of total carbon allocated to roots from growth and maintenance respiration (ΣR) were combined (Column 6). Gross primary production (GPP)[1] (Column 8) and total net primary production (NPP)[2] (Column 9) were derived by summing values from appropriate columns to calculate the ratio of NPP/GPP. All units are in g C m^{-2} year^{-1}.

Stand no. (1)	NPP$_a$ (2)	$R_{g(a)}$ (3)	$R_{m(l)}$ (4)	$R_{m(s+b)}$ (5)	ΣR_{root} (6)	NPP$_{root}$ (7)	GPP (8)	NPP (9)	NPP/GPP (10)
1	525	131	97	334	156	156	1399	681	0.49
1a	585	146	108	262	228	228	1557	813	0.52
2	580	145	107	453	190	190	1665	770	0.46
3	875	219	162	653	247	247	2403	1122	0.47
4	255	63	47	278	118	118	879	373	0.42
5	75	19	13	88	84	84	363	159	0.44
6	45	11	8	84	77	77	302	122	0.40
7a	599	149	245	400	511	511	2415	1110	0.46
7b	750	187	291	267	518	518	2531	1268	0.50
7c	1291	323	457	628	370	370	3439	1661	0.48
8	457	114	85	186	202	202	1246	659	0.53
9	690	–370–		210	880	320	2470	1010	0.41

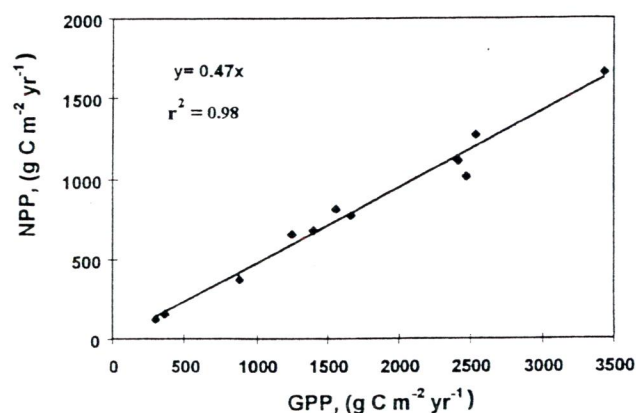[1] GPP = (2) + (3) + (4) + (5) +(6) + (7).

[2] NPP = (2) + (7).

Figure 1. Regression of NPP to GPP forced through the origin. The slope of the relationship is 0.47 with a standard deviation of 0.04 for the forests analyzed in Table 2.

atmosphere from undisturbed forest ecosystems, and particularly those receiving atmospheric nitrogen deposition in excess of background values (Gifford 1994, Thornley and Cannell 1996). If, on the other hand, the release of nitrogen (or other nutrients) from litter were to lag behind increases in plant maintenance respiration, photosynthesis and growth of new foliage might both be limited and the net ecosystem carbon exchange to the atmosphere increased (Comins and McMurtrie 1993, Wang and Polgase 1995).

Given that we can now calculate GPP for forest stands with considerable confidence, recognition that the NPP/GPP ratio is stable allows us to make progress in modeling forest stands. Assuming that the models from which we estimate canopy

CO_2 uptake are giving acceptably accurate results, the use of a constant ratio of NPP/GPP reduces the difficulty of calculating NPP from GPP to that of carbohydrate allocation. Landsberg and Waring (1997) argue that the errors involved in determining carbohydrate allocation are likely to be much smaller than the errors that may arise from attempting to make continuous calculations of respiration for (simulated) stands growing under a range of conditions. Clearly, research must continue on all aspects of carbon fixation, utilization, and allocation, but robust simplifications of the type presented here greatly increase the utility and value of models, as well as provide clear hypotheses that can be tested by measurement.

We note that the data assembled in this paper also provide a useful insight into the problem of radiation conversion efficiency (ε). Radiation conversion efficiency has been determined for aboveground production, with values for forests and plantations ranging from about 0.2 to 2.0 g (dry mass) MJ^{-1} (absorbed radiation), but commonly clustering round 1–1.5 g MJ^{-1} (see review by Landsberg et al. 1996). There appear to be two major reasons for the large variation in ε. First, there are constraints on stomata that limit the diffusion of CO_2 and the effective conversion of APAR into photosynthate. Stomatal limitation on the effective conversion of APAR may approach 80% in some evergreen arid, cold woodlands (Runyon et al. 1994). Second, restricting the calculation of ε to aboveground NPP, rather than total NPP, leads to additional variation in results. Examination of the data in Table 2 indicates that the ratio of root NPP to aboveground NPP ranges from about 0.3 to 1.7, showing clearly that the aboveground growth patterns of trees are strongly affected by the proportion of the carbon fixed that is allocated to root growth and turnover. This variation in allocation of NPP has considerable implications for all

attempts to interpret aboveground growth in terms of applied treatments, or any other factors assumed to affect forest growth. From the modeling point of view, it may be more useful to calculate GPP and use knowledge about growing conditions to estimate the proportion allocated to roots, and hence aboveground growth (see Landsberg and Waring 1997).

Acknowledgments

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