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Commentary

The assessment of NPP/GPP ratio

Joe J. Landsberg¹, Richard H. Waring^{2,4} and Mathew Williams³

¹'Withycombe' Church Lane, Mt Wilson, NSW 2786, Australia; ²College of Forestry, Oregon State University, Corvallis, OR 97330, USA; ³Centre for Sustainable Forests and Landscapes, School of GeoSciences, NCEO, The University of Edinburgh, Edinburgh EH9 3FF, UK; ⁴Corresponding author (richard.waring@oregonstate.edu)

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In 1998, we obtained a close linear relationship between gross primary biomass production (GPP), the total mass of carbon fixed annually by photosynthesis, and net primary biomass production, designated (NPP) (Waring et al. 1998). Collalti and Prentice (2019) (henceforth denoted C&P) recently asserted that Waring, in that 1998 paper, hypothesized that this constant NPP/GPP ratio was 'universal across biomes, tree species and stand ages'.

This is not correct. We said, in the abstract of that paper: 'To search for possible common relationships (between GPP and respiration), we assembled annual carbon budgets from 12 forest sites ... analysis indicated that the total NPP/GPP ratio was conservative (0.47 ± 0.04). This finding supports the possibility of greatly simplifying forest models.' We were—and are—well aware that the ratio we obtained is an empirical approximation, which is likely to vary in different stands and under different conditions. We did not postulate that it might be universal across biomes, tree species and ages; that would have been a legitimate, testable hypothesis, but we are not aware that anyone has stated it in that way. However, the fact that the constant ratio was subsequently questioned and tested by a number of authors (Medlyn and Dewar 1999, Mäkelä and Valentine 2001, DeLucia et al. 2007, Litton et al. 2007, among others) in relation to a range of forests and conditions, suggests that they considered the hypothesis of its universal application to be implicit.

The various investigations have yielded a range of values, mostly between 0.4 and 0.6. C&P examined data from more than 200 stands, from which they obtained an average NPP/GPP ratio of 0.46, which was 'statistically indistinguishable from that given by Waring et al.' However, the values varied from 0.22 to 0.79, a total range, they said, which is too large to be

disregarded. They concluded that the hypothesis of a universal constant or slightly variable ratio of NPP to GPP should now be rejected.

If we accept that the empirical relationship established by Waring et al. (1998) provides the basis for a hypothesis stating that the relationship between NPP and GPP is constant and universal across forest stands and ecosystems, then the evaluation of that relationship by C&P, who included in their analysis most of the other studies that addressed the question, constitutes a legitimate test of the hypothesis. But, since we never proposed the constant ratio as a universal hypothesis, there is no question of rejecting that 'hypothesis' and the issue becomes 'should the use of the constant ratio be discontinued because of the range of values found by C&P?'. We do not think so, and provide citations and analysis, below, to support this opinion.

Stand-level models of forest growth and productivity, intended for use over large areas and long periods (months to years), must be based on relatively simple relationships. The success of such models has been widely demonstrated (e.g. Coops et al. 1998, Mummery and Battaglia 2001, Landsberg et al. 2003). These relationships may be established empirically or derived from detailed models of light interception and photosynthesis at leaf, stand or canopy level (e.g. Williams et al. 2001). The respiration term to yield NPP should be at the same level. In the 3-PG model (Landsberg and Waring 1997), which was written as a deliberate attempt to bridge the gap between conventional empirical (mensuration-based) growth and yield models and process-based carbon balance models (Landsberg and Sands 2011), a light-use efficiency factor is used, with the light intercepted by forest canopies, to calculate GPP.

Cannell and Thornley (2000) have argued that it would be more satisfactory if a stable value for the NPP/GPP ratio emerged from analyses of respiration in relation to GPP based on appropriate physiological mechanisms, rather than using an empirically established value (see comment by Ryan and Asao 2019). In developing 3-PG we needed a model of tree and stand respiration that could be scaled up to the level of the canopy photosynthesis model, but since we lacked—and still lack—a respiration model based on such analyses, we used the constant NPP/GPP ratio described by Waring et al. (1998).

Pending the development of an appropriate respiration model and the use of a constant, or nearly constant, NPP/GPP value in large-scale ecosystem models arguably remains the best available option. It will lead to errors in particular areas, but, on average, the results are likely to be better than those that might be obtained when attempts are made to use a detailed model of respiration, because of the challenge in estimating many parameters accurately. When such a model becomes available, it is likely that it will only be applicable to simple and well-specified systems (e.g. monospecific plantations), and even for those it is likely that large data inputs will be required to describe the system and prevailing environmental conditions. However, a process-based respiration model—provided it includes terms to quantify the downward flux of carbon and autotrophic and heterotrophic soil respiration (see later discussion)—could be used to identify the reasons for the variations in respiration in different stands and conditions, allowing the development of simplified relationships that could be used with stand-level photosynthesis models. Some progress in developing mechanistic models has been made (Minchin et al. 1993), but most are still theoretical (e.g. Lemaire and Millard 1999).

C&P consider several factors likely to influence the NPP/GPP ratio and cause it to vary. These include carbohydrate reserves, which vary with tree age, seasonally, and with growing conditions and responses to disturbance, temperature, soil fertility and drought. They note that belowground allocation of carbon includes the allocation to fine roots and the exudation of low molecular weight organic compounds that are unaccounted for by 'classical' respiration measurements.

We pause here, before going on to discuss soil and root respiration in more detail, to provide support for our assertion that ratios of NPP/GPP at seasonal and annual time steps are unlikely to exceed values of 0.6 or fall much below 0.4. We first looked at the range of values in NPP/GPP used in the forest growth model 3-PG at sites where GPP was estimated from continuous measurements of CO₂ exchange above forest canopies, often along with aboveground growth and estimates of leaf area index (LAI). We found that the default NPP/GPP ratio (0.47) gave good agreement between the predicted and observed values in most, if not all, cases when used at seasonal and annual time steps, but not daily. These comparisons included two drought-prone Mediterranean woodlands

(Nolè et al. 2013), young and old ponderosa pine forests (Law et al. 2000, 2001) and an intermediate-aged Douglas-fir stand (Waring et al. 2008). We progressively increased and decreased the ratios of NPP/GPP from the default value for the old ponderosa and intermediate-aged Douglas-fir stands where information on growth rates and canopy leaf area indices was available. Although NPP/GPP could vary ± 0.1 without much effect on GPP, resulted in linear shifts in growth rates and LAI. This kind of sensitivity analysis is insufficient to rule out variation in the NPP/GPP ratios at all forested sites, but it raises doubts that extreme variation is likely.

A more rigorous approach to assessing variation in NPP/GPP ratios is to cross-check all measurements of CO₂ fluxes and ratios. An international group of scientists concerned with closing the CO₂ balance found many inconsistencies in data sets acquired at over 500 sites where fluxes of CO₂ were continuously monitored for a series of years (Luysaert et al. 2009). They cross-checked biometric measurements of NPP and attempted to distinguish autotrophic (R_a) from heterotrophic (R_h) sources of respiration. They compared NPP/GPP, R_h /NPP and two ecosystem respiration (R_{eco}) ratios, R_h/R_{eco} and R_{eco} /GPP, for consistency. They found only 16 sites out of 529 where the data available closed the CO₂ balance. The derived estimate of the NPP/GPP ratios where closure was complete was 0.51 ± 0.02 and for incomplete closure, 0.50 ± 0.01 . We encourage a similar analysis at the 200 sites reported by C&P.

Model–data fusion methods can combine multiple observations of the carbon cycle with a mass balance model to constrain NPP/GPP ratios. For site-level analyses with local observations, Williams et al. (2005) estimated an NPP/GPP ratio of 0.53 for a ponderosa pine stand, and Smallman et al. (2017) estimated 0.60 for loblolly pine and 0.42 for Sitka spruce. For global $1 \times 1^\circ$ resolution analyses using satellite observations, the most likely NPP/GPP ratios obtained from this form of inverse modeling were 0.42–0.44 in the wet tropics, 0.45–0.50 in the dry tropics, 0.47–0.50 in temperate zones (23–55° N/S) and 0.49–0.50 in high-latitude (>55° N/S) areas (Bloom et al. 2016). These analyses suggested there was only a small probability that these ratios might fall outside 0.4–0.6. Outside this range the mass balance modeling struggled to reconcile observed carbon stocks and their likely turnover times (the model links these to NPP) with expected rates of photosynthesis (GPP), given observed LAI and climate.

In the following paragraphs of this commentary we review briefly, and provide some additional comment on, the important question of belowground allocation of carbon by trees.

Soil respiration (R_{soil}) has often been assessed with chambers (Pumpanen et al. 2004), which measure the flux of CO₂ from the soil surface but cannot fully separate the contributions of roots and microbial decomposition of soil organic matter, including mycorrhizal activity around root surfaces. Soil

respiration measurements therefore provide, at best, approximate values from which the belowground flux of carbon can be deduced. Hanson et al. (2000), reviewing methods of separating soil and microbial contributions to soil respiration, found that the average root contribution to total soil CO₂ efflux was about 45%—this implies that heterotrophic respiration contributes about 55% of soil respiration to the CO₂ efflux measured from flux towers over forests (see Luysaert et al. 2009). Hanson et al. (2000) as well as Hopkins et al. (2013) say that isotopic measurements of the contribution of root and rhizosphere organisms are the best way of separating root respiration from total soil respiration (e.g. Drake et al. 2019a, 2019b).

A seminal paper on belowground allocation of carbon was provided by Högberg et al. (2001), who carried out a large-scale girdling experiment in a boreal pine forest. They found that girdling—stripping the stem bark to the depth of current xylem, which stops the supply of current photosynthates to roots—rapidly reduced soil respiration. Comparisons with control plots indicated that more than 50% of soil respiration was contributed by root mycorrhizae and exudate (heterotrophic) respiration. There were marked seasonal patterns in the fluxes (see also Högberg et al. 2008, 2009) and clear indications of strong coupling between soil respiratory activity and tree canopy photosynthesis. Liu et al. (2006) found that soil respiration in a temperate deciduous forest showed an independent component, linked to canopy photosynthesis. Both GPP and R_s are affected by temperature but extreme drought, subfreezing temperatures (Hadley 2000) and defoliation all halt export of photosynthate to roots and cause a weakening in the relationship between temperature and GPP and soil respiration (Andersen et al. 2005). Consistent findings emerged from a review of literature on forest carbon budgets by Litton et al. (2007): their analysis indicated that total belowground carbon flux in forest ecosystems generally increased with increasing aboveground NPP, but the proportion of assimilate going to root systems decreased with increasing water and nutrient resources and increased when nutrients (particularly) were in short supply. In the latter case, potentially more assimilate is likely to be allocated to mycorrhizal fungi and root exudates as atmospheric concentrations of CO₂ continue to increase (Treseder 2004, Fransson 2012).

The point that emerges from these and other studies is that attempts to model respiration in trees and forest ecosystems as a step towards estimating NPP from GPP must include not only models of the respiration process per se, in foliage, stems and roots, but also the distribution to all sinks and in particular the flow of carbon from canopies to root systems (F_{\downarrow})—sometimes called total belowground carbon flux.

Eq. (1) provides a summary of the processes involved:

$$P_n = P_g - (R_f + R_w + F_{\downarrow}), \quad (1)$$

where P_n is the net primary biomass production, P_g is the gross primary carbohydrate production, R_f is the foliage respiration and R_w is the respiration from woody tissue (not including roots). Downward flow (F_{\downarrow}) has to be partitioned between root growth and autotrophic respiration (R_r) and the fraction (R_e), which goes to root exudates and supports heterotrophic mycorrhizal respiration (Eq. (2)). That fraction, as we noted earlier from Hanson et al. (2000), may be more than 50% of F_{\downarrow} (see also Högberg et al. 2008, 2009):

$$F_{\downarrow} = R_r + R_e \quad (2)$$

We note the important point that F_{\downarrow} is a function of soil nutrient status, soil water status, soil temperature and seasonal factors affecting canopy photosynthesis.

For evidence of seasonality, see Högberg et al. (2009) who found strong seasonal trends but noted hysteresis loops in the relationship between soil respiration ($R_r + R_e$) and soil temperature. See also Liu et al. (2006), cited earlier.

It has been known for a long time (Chapin 1980) that plants growing in soil with ample nutrient supplies use relatively less carbon for root growth than plants growing in soils where nutrient availability is low. This point was reinforced by Litton et al. (2007). They found, from statistical analyses of a large number of forest growth and productivity studies, in which above- and belowground components of growth were measured, or from which they could be estimated, that increased nutrient availability increased partitioning to aboveground growth and decreased partitioning to belowground growth. A similar pattern pertained for soil water: better water availability resulted in a higher proportion of carbon partitioned to aboveground growth and vice versa, although the results were not as consistent as those for nutrients. (In the 3-PG model, allocation of carbon to root growth and related belowground sinks is based on soil nutrient and water availability, but that is done after NPP has been calculated.)

Biomass does not appear to be a good predictor of carbon flux in forests because measurements of this entity omit the R_e term (Litton et al. 2007). This point emerges from Eqs (1) and (2). C&P also note that 'biomass production and NPP differ because part of NPP can be allocated to organic compounds that are not used for growth . . .'. This includes, presumably, R_e . Vicca et al. (2012) introduced the term 'biomass production efficiency', which is essentially the ratio $P_n/(P_g - (R_f + R_w + R_r))$. The R_e term is seldom (if ever) measured in forest production studies and therefore becomes a source of error, as they recognized.

It is clear, from the literature we have considered here—albeit briefly—that the downward flux of carbon to tree roots is an important determinant of NPP. In our original paper (Waring et al. 1998), belowground NPP by roots was not measured directly; instead a relationship based on leaf-litter fall and CO₂

efflux from the soil (Raich and Nadelhoffer 1989) was used to estimate total belowground allocation (net production + growth and maintenance respiration). The fraction of NPP allocated to belowground sinks was calculated to vary from a minimum of 22% to a maximum of 63% in the sample of 12 forest stands ranging in productivity by more than 10-fold. Many assumptions were made, but belowground allocation was assessed and included in the calculations of NPP and GPP. Omitting consideration of total belowground allocation has undoubtedly been a significant source of error in many estimates of both NPP and GPP.

It is clear that the emerging importance of the R_e term (Eq. (2)) means that models aimed at calculating NPP of forest ecosystems in terms of carbon fluxes, and predicting CO_2 fluxes in relation to regional- and global-scale CO_2 budgets, must include that term. Soundly based, mechanistic respiration (sub)models that allow calculation of respiratory fluxes from foliage and stems will remain essential components of such ecosystem models, but without the ability to calculate F_{\downarrow} , there will still be a significant unquantified flux that will be a source of error and uncertainty. We do not, at this stage, see a path to calculating F_{\downarrow} on the basis of biophysical processes, but there are indications in the literature describing girdling and isotope experiments that there is, or soon will be, enough information available to allow the development of empirical functional forms of the relationships indicated in defining downward flux (F_{\downarrow}). Similarly, it should be possible to partition F_{\downarrow} into R_r and R_e , for different situations and seasons. Heterotrophic soil respiration, which is not immediately associated with F_{\downarrow} of carbon in trees and associated symbiotic mycorrhizal respiration, presumably can be quantified on the basis of the decomposition rates of soil organic matter and dead material in soils, the latter determined almost entirely by the temperature and water content of forest soils.

In summary, we consider that estimates of NPP/GPP ratios below 0.4 and above 0.6 are unlikely, in part resulting from incomplete assessment of NPP that is allocated to mycorrhizal and free-living soil fungi and in the context of our understanding and modeling of carbon budgets at ecosystem scale. The NPP/GPP ratio must make sense in the context of full carbon budgets at ecosystem scale—and extreme values of this ratio are hard to reconcile (although not impossible—we still have some work to do here). There also remain challenges in separating auto- from heterotrophic respiration, but experimental approaches with labeled isotopes hold considerable promise. If more detailed mechanistic models are sought to account for variability in the ratio, then belowground allocation and especially root exudation should be of crucial importance.

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