



Review

Is NPP proportional to GPP? Waring's hypothesis 20 years on

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Gross primary production (GPP) is partitioned to autotrophic respiration (R_a) and net primary production (NPP), the latter being used to build plant tissues and synthesize non-structural and secondary compounds. Waring et al. (1998; *Net primary production of forests: a constant fraction of gross primary production?* *Tree Physiol* 18:129–134) suggested that a NPP:GPP ratio of 0.47 ± 0.04 (SD) is universal across biomes, tree species and stand ages. Representing NPP in models as a fixed fraction of GPP, they argued, would be both simpler and more accurate than trying to simulate R_a mechanistically. This paper reviews progress in understanding the NPP:GPP ratio in forests during the 20 years since the Waring et al. paper. Research has confirmed the existence of pervasive acclimation mechanisms that tend to stabilize the NPP:GPP ratio and indicates that R_a should not be modelled independently of GPP. Nonetheless, studies indicate that the value of this ratio is influenced by environmental factors, stand age and management. The average NPP:GPP ratio in over 200 studies, representing different biomes, species and forest stand ages, was found to be 0.46, consistent with the central value that Waring et al. proposed but with a much larger standard deviation (± 0.12) and a total range (0.22–0.79) that is too large to be disregarded.

Keywords: autotrophic respiration, carbon-use efficiency, forest ecosystem, modelling, primary production.

Introduction

Forest carbon budgets are dominated by two opposing fluxes: photosynthesis (or gross primary production, GPP) and autotrophic respiration (R_a). The remainder is net primary production (NPP), which accrues to tissues (eventually becoming detritus and respired heterotrophically) and to a variety of non-structural compounds that help to maintain plant and rhizosphere function (Chapin et al. 2006). Estimation and modelling of the net carbon balance of forests requires accurate estimation of how GPP is partitioned, because a small relative error in this partitioning could lead to a larger relative error in the carbon balance (DeLucia et al. 2007, Hermle et al. 2010).

However, there is still large uncertainty about how GPP is partitioned in forests. One school of thought emphasizes constancy in the ratio of NPP to GPP.

McCree and Troughton (1966) argued that this ratio should be more-or-less invariant (in plants generally) with respect to ageing, CO₂ and temperature. Van Oijen et al. (2010) suggested, moreover, that it should be stoichiometrically constrained between 0.55 and 0.6. Gifford (1995, 2003) and Van Oijen et al. (2010) emphasized that the substrate for respiration originates from photosynthesis and so R_a must inevitably depend on GPP, at least when averaged over long enough periods; Gifford (1995) provided experimental evidence (from wheat) in support of the idea of a near invariant of NPP to GPP. Waring et al. (1998) (hereafter W98) subsequently reported, in this journal, that the NPP:GPP ratio in a sample of 12 temperate and boreal forest stands was tightly constrained, with a central value of 0.47 ± 0.04 (here and elsewhere, ‘±’ denotes one standard deviation) and a narrow range from 0.40 to 0.52. This claim of a constant NPP:GPP

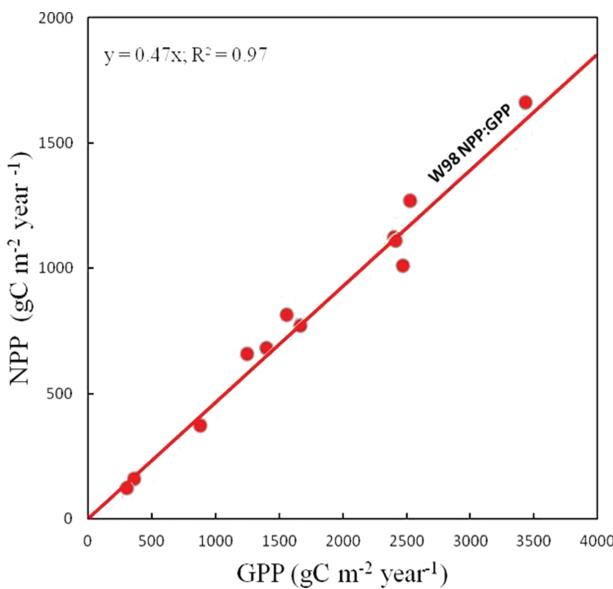


Figure 1. Regression of NPP versus GPP forced through the origin for 12 forest sites (from Waring et al. 1998, Table 2).

ratio near 0.5 was re-iterated in the recent review by Waring and Landsberg (2016). The close relationship of NPP to GPP in the data analysed by W98 is illustrated in Figure 1.

Gifford (1995) and W98 noted that for modelling purposes, assuming invariance would be more realistic than treating respiration as if it were independent of GPP. A universal value of the NPP:GPP ratio would indeed be convenient for analysis and modelling, because it would allow straightforward estimation of NPP, whose measurement requires either destructive sampling or allometric approximations, from GPP. Gross primary production can be estimated either from remote sensing using a light-use efficiency model, at a time scale of around a week (Heinsch et al. 2006) or on a sub-daily basis by partitioning the net ecosystem CO₂ exchanges measured by the eddy covariance network (Beer et al. 2010). A number of vegetation models [including all published versions of 3-PG, Landsberg and Waring 1997; CenW (as one option), Kirschbaum 2005; PROMOD, Sands et al. 2000; C-Fix, Veroustraete et al. 2002; early versions of TRIPLEX, Peng et al. 2002; FullCAM, Richards and Ewans 2004; HyLand, Levy et al. 2004; 4C, Lasch et al. 2005; BASFOR, Van Oijen et al. 2005; TOPS-BGC, Nemani et al. 2009; ForCent, Parton et al. 2010; G'DAY (as one option), Dezi et al. 2010; Picus, Seidl et al. 2012; and early versions of 3D-CMCC FEM, Collalti et al. 2014] have assumed a constant NPP:GPP ratio. W98 has been cited in many carbon balance studies (in the Web of Science search engine, the search string 'Waring et al. 1998' yielded 422 returns and in Google Scholar, 596 returns; both accessed 1 March 2019). A constant NPP:GPP ratio has been invoked in local, regional and global carbon storage assessments (e.g., Lenton and Huntingford 2003, Magnani et al. 2007, Zhang et al. 2006, Zha et al. 2009, Peichl et al. 2010, Sun et al. 2014),

considered as a benchmark value (e.g., Griffs et al. 2004), described in textbooks (Landsberg and Sands 2010, Ågren and Andersson 2012) and applied in one version of the MODIS NPP product (Jay et al. 2016).

A number of empirical and theoretical studies carried out since W98 have thus converged on the insight that R_a should not be regarded as a process independent of GPP, but rather regarded as a relatively conservative fraction of GPP, and numerous ecosystem models have adopted the approximation that R_a is a constant fraction of GPP. The two fluxes are indeed closely coupled, and the ratio of NPP to GPP is therefore more nearly constant than one would expect if they were independent. On the other hand, a growing body of research since W98 has emphasized variation in the NPP:GPP ratio, and focused on identifying its controls. Responding to W98, Medlyn and Dewar (1999) argued for a broader range of NPP:GPP ratios (0.31–0.59) than was reported there. They noted that the methods used by W98 to calculate NPP may have predetermined the finding of a near-invariant NPP:GPP ratio. They concluded that the hypothesis of a fixed NPP:GPP ratio, although 'having some basis in theory', was just one option for modelling—and not a desirable avenue to pursue in the absence of experimental support.

In this paper we review studies on the partitioning of forest GPP since the publication of W98. Some of these studies have pointed to an approximately constant ratio of NPP to GPP, others to a variable one. To some extent this has been a question of emphasis (is the glass 'half full' or 'half empty'?). Thus, some publications have reported negative results (e.g., no effect of forest type or stand age on the ratio), others have reported such effects while downplaying their importance, while others have focused on the importance of considering these effects. We summarize results of these various studies approximately chronologically within each of three broad categories of study, according to their principal focus on effects of forest type and stand age, effects of climate (temperature and drought) or effects of site fertility, disturbance and management. We finally summarize data on NPP:GPP ratios in a new data set compiled from over 200 studies, representing different biomes, species and stand ages, and draw some general conclusions about the state of knowledge and research needs.

Definitions of terms

GPP is the balance between carbon fixed through photosynthesis and carbon lost through photorespiration, expressed per unit ground area and time (Wohlfahrt and Lu 2015). NPP is GPP minus autotrophic respiration (Clark et al. 2001). Biomass production (BP; Vicca et al. 2012) is the part of NPP that is used for biomass growth (taken to include litter and fruit production). Biomass production and NPP differ because part of NPP can be allocated to organic compounds that are not used for growth, including non-structural carbohydrates (NSCs; including

starch, sugars and other polysaccharides), labile root exudates (primarily organic acids) that support biological activity in the rhizosphere and secondary metabolites (including biogenic volatile organic compounds) that are involved in signalling, defence against pathogens and herbivores or protection of tissues against thermal oxidative stress. Following the definitions by Roxburgh et al. (2005), BP is constrained to be always zero or positive (tissues consumed by herbivores, for example, are considered to be part of BP), while NPP can be potentially negative ($R_a > GPP$) for limited periods. Over periods of years, NPP must equal or exceed BP.

Gifford (1995) proposed the term 'carbon use efficiency' ($CUE = 1 - R_a/GPP$), which is equivalent to the NPP to GPP ratio as defined by W98. Vicca et al. (2012) more recently introduced the term 'biomass production efficiency' ($BPE = BP/GPP$), which is equivalent to 'gross growth efficiency', as defined in the comprehensive review—across all kinds of organisms, both autotrophic and heterotrophic—by Manzoni et al. (2018). Although in general $BPE \leq CUE$, none of the papers reviewed here, apart from Vicca et al. (2012), Fernández-Martínez et al. (2014) and Campioli et al. (2015), make a clear distinction between BP and NPP—compelling us, for comparison with the wider literature, to treat BPE and CUE as if they were synonymous although they clearly are not.

As data on 'NPP' have often been obtained by biometric measurements, some reported values may be better considered as estimates of BP rather than NPP (see also Malhi et al. 2015). However, even if the difference is usually small, the distinction is worth making in future research and should allow better quantification than is possible based on the current literature.

Studies examining effects of forest type and stand age

Law et al. (1999) compared two patches at different successional stages (45 and 250 years old) in a *Pinus ponderosa* (Douglas ex C. Lawson) forest in a summer-dry climate in Oregon, USA. They found the same NPP:GPP ratio (0.45) in both patches. Cannell and Thornley (2000) and Thornley and Cannell (2000) showed a relatively stable ratio of R_a and GPP (implying a range of only 0.55–0.65 for the NPP:GPP ratio) over an age range of 0–60 years. However, they noted that assuming a single constant value in models might overlook both differences among sites and variations from year to year. Amthor (2000), analysing 30 years of studies on the NPP:GPP ratio (obtained by subtracting respiration estimates from GPP), concluded that it ranged from 0.20 to 0.65, spanning from the maximum growth rate per unit of photosynthesis and minimum tissues maintenance costs (0.65) to limited growth (if any) and maximum maintenance costs (0.2). He reported the lowest values for moist tropical forests, and the highest value for a temperate *Fraxinus* plantation.

Mäkelä and Valentine (2000) applied a process-based model of forest growth in conjunction with measurements from a *Pinus*

sylvestris (L.) forest. They found that increasing sapwood mass with increasing height and age increased the respiring biomass, and thus R_a . Their model estimated a decline in the NPP:GPP ratio from 0.6 to 0.2 as tree height increased from 5 to 30 m. They concluded it was unlikely that R_a could be a constant fraction of photosynthesis over the full time course of stand development. Later, Vanninen and Mäkelä (2005), also studying a *P. sylvestris* (L.) forest, measured a reduction in the NPP:GPP ratio, from 0.65 to 0.45, with increasing tree height.

Ryan et al. (2004) used data from an experimental *Eucalyptus saligna* (Sm.) forest to explicitly challenge the long-standing forest dynamics paradigm of Kira and Shidei (1967) and Odum (1969), in which increasing R_a was assumed to drive a decline in the NPP:GPP ratio with stand age. Ryan et al. found instead that an age-related decline in GPP was accompanied by a decline in R_a . The NPP:GPP ratio did vary with stand age, but only slightly, from 0.66 at age 2 years to 0.62 at age 6 years. They concluded that NPP:GPP should be considered 'roughly' constant and effectively independent of biomass or stand age.

Litton et al. (2007) reviewed the constancy, or otherwise, of NPP:GPP in the literature available at the time, and their study was updated with new data by Ise et al. (2010). Litton et al. conducted a meta-analysis of annual carbon budgets based on 63 forest ecosystems varying in fertility, structure and stand age. They found a highly significant correlation between R_a and GPP ($R^2 = 0.95$, $n = 23$, $P < 0.01$). The NPP:GPP ratio was approximately constant across sites (0.43 ± 0.02), but the total range was from 0.29 to 0.58. Three outliers (two boreal, one tropical) fell for 'unknown reasons' in the low range of 0.29–0.34. No effect of either stand age ($n = 4$) or soil fertility ($n = 7$) was found, probably due to the paucity of data.

De Lucia et al. (2007) analysed published data from 60 forest sites with stand ages varying from 5 to 500 years. They found that the NPP:GPP ratio, largely based on biometric estimates of BP standing in for NPP, varied substantially among biomes and age classes. The highest value (0.83) was found in a 5-year-old plantation of *Populus nigra* (L.), experimentally exposed to a high CO₂ concentration. The lowest (0.22) was found in a 115-year-old *Picea mariana* (Mill.) stand. Figure 2, based on the data analysed by De Lucia et al., shows a clear difference among biomes—with low ratios of NPP:GPP in boreal forests and high ratios in temperate deciduous forests.

Thornley (2011) found the NPP:GPP ratio to vary from 0.5 to 0.6 and argued that this ratio is conservative among ecosystems, but that it varies with stand age depending on growth efficiency and recycling fraction. Goulden et al. (2011), analysing biometric data from a chronosequence of seven even-aged boreal forest stands, found that the NPP:GPP ratio decreased from ~0.5 to ~0.3 with increasing stand age. Tang et al. (2014) found variability in the NPP:GPP ratio across biomes (obtained mostly from biometric BP measurements) from 0.3 to 0.45, but no significant correlation between

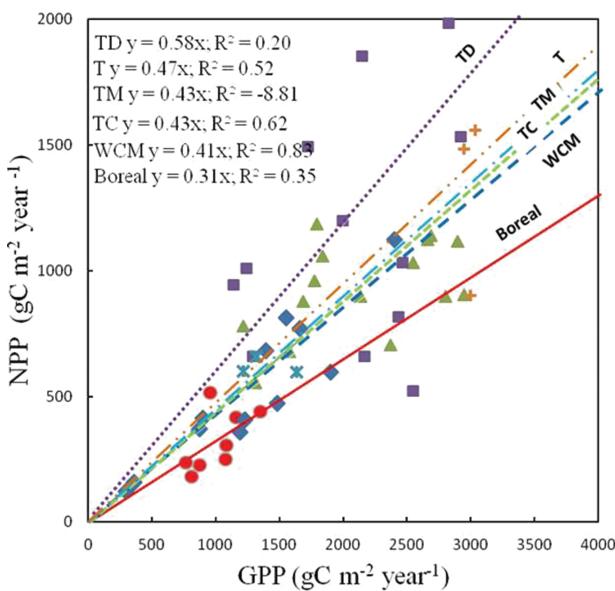


Figure 2. Regressions of NPP versus GPP forced through the origin for different forest types, from data in DeLucia et al. (2007). Circles represent boreal; squares, temperate deciduous (TD); triangles, temperate coniferous (TC); diamonds, west coast maritime (WCM); crosses, temperate mixed (TM); plus signs, tropical (T).

NPP:GPP and age—suggesting that declining GPP during stand development (due to hydraulic limitations) is paralleled by decreasing R_a as proposed by Ryan et al. (1997b) and Drake et al. (2011). They also speculated that biome-specific differences might be due to soil fertility and/or temperature.

Studies examining effects of temperature

Saxe et al. (2000) noted that the short-term relationship of respiration to temperature, as observed in the laboratory and driven by enzyme kinetics, is likely to be unrepresentative of the long-term behaviour of respiration because the crucial acclimatory response of the base rate to temperature is missing. They argued, instead, that acclimation should cause NPP to be proportional to GPP.

Dewar et al. (1999) noted that a short-term increase in R_a with temperature could be fuelled by non-structural carbon reserves, whereas in the longer term R_a must be constrained by the supply of substrates from photosynthesis. They accepted the idea that NPP:GPP might be conservative. However, they expressed caution with regard to applying a single value across a wider range of temperatures (and other environmental factors) than were considered in W98.

Gifford (2003), analysing data (obtained in some cases from R_a , in others from biometric measurements) from various earlier works (Gifford 2003, Table 3 and references therein), noted that while the average NPP:GPP ratio for field-grown trees varies only slightly (0.47 ± 0.05), glasshouse-grown seedlings in controlled environments generally show higher average values (0.58 ± 0.03). Citing Tjoelker et al. (1999), he suggested

that (i) species may acclimate to increasing temperature to different extents and (ii) that the overall NPP:GPP ratio is likely to decrease slightly with increasing temperature.

Piao et al. (2010), analysing the global forest carbon budget data set ($n = 104$) compiled by Luyssaert et al. (2007), considered variations of R_a , obtained by different methods, in relation to mean annual temperature (MAT), NPP, total biomass, height, maximum Leaf Area index (LAI) and stand age. This analysis indicated a non-linear relationship of the R_a :GPP ratio to MAT across latitudes ($R^2 = 0.43$, $P = 0.03$): decreasing at first, levelling off around ~ 11 °C and thereafter increasing again. This analysis implies a range in the NPP:GPP ratio from 0.25 to 0.42, with a maximum at ~ 11 °C. No relation to forest age was found outside the MAT range of 8–12 °C.

Keith et al. (2010), in common with Dewar et al. (1999), noted that W98's methods for estimating GPP and NPP were not independent, thus potentially biasing W98's conclusion towards a constant ratio. They noted that asynchrony between the production and utilization of assimilated and stored carbohydrates must inevitably produce interannual variations in the NPP:GPP ratio in response to a temporarily variable climate. In a global sample of 27 forests, they found the NPP:GPP ratio to vary between 0.29 and 0.61, being non-linearly related to GPP (see also Malhi et al. 2015), with MAT and solar radiation accounting for about half of the variation.

Chambers et al. (2004) and Metcalfe et al. (2010), analysing data from a throughfall exclusion experiment in Amazonian rainforest, found NPP:GPP ratios ranging from 0.24 ± 0.04 for experimentally drought trees to 0.32 ± 0.04 for control trees.

In an assessment of the carbon balance in a *Fagus sylvatica* (L.) forest over a 5-year period, Wu et al. (2013) found that NPP:GPP varied from 0.32 to 0.4, due to asynchronous interannual variations in GPP and NPP linked to interannual variability in climate.

Studies examining effects of soil fertility, disturbance and management

Malhi et al. (2009, 2011, 2015) and Malhi (2012) estimated the NPP:GPP ratio of primary tropical forests to be in the range from 0.3 to 0.4, varying because of disturbances and across different soil fertility classes. They also argued that their values were likely underestimated to some extent because of missing components of NPP, in particular the poorly quantified transfer of carbon to the rhizosphere through root exudates and transfers to mycorrhizal symbionts.

Maier et al. (2004) found that experimentally increasing nutrient availability in a *Pinus taeda* (L.) plantation had no effect on the NPP:GPP ratio. In contrast, Giardina et al. (2003) and Vicca et al. (2012) found that site fertility was a major control of this ratio to GPP, which was found to range from ~ 0.4 to ~ 0.6 . Vicca et al. (2012) described temperate forests as being usually more fertile than boreal forests and consequently having

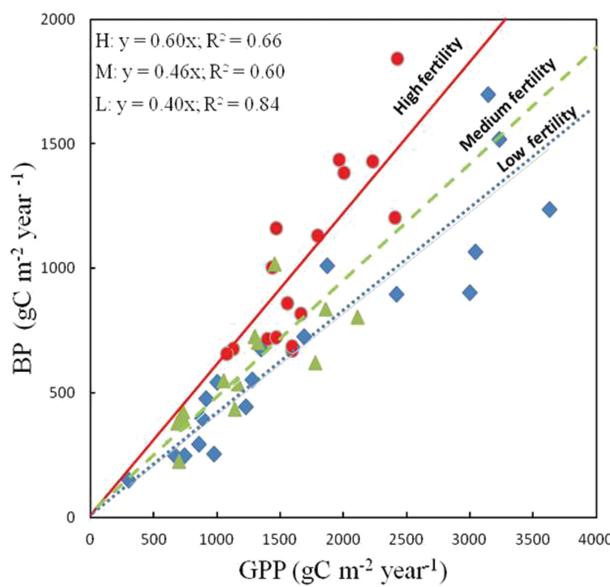


Figure 3. Regressions of BP versus GPP forced through the origin at different level of soil fertility, from data in Vicca et al. (2012). Circles, squares and triangles represent different soil nutrient availability classes, 'H', 'M' and 'L' refers to high-, medium- and low-soil fertility, respectively.

a higher BP:GPP ratio. Forest management emerged as the next best predictor of the BP:GPP ratio, followed by stand age. Figure 3 shows the strong effect of site fertility in the data of Vicca et al. Doughty et al. (2018), analysing 14 tropical forest sites across different rainfall and soil regimes in Amazonia and the Andes, found no significant relationship between temperature and CUE (see also Malhi et al. 2015), but did find lower CUE in less fertile sites.

Campioli et al. (2015) analysed ratios of BP to GPP in 131 managed and unmanaged sites, mainly in Europe and North America. They found a constant ratio (0.46 ± 0.01) in unmanaged forests and a higher ratio in managed forests (0.53 ± 0.03). They described how management can shift carbon allocation patterns to favour above-ground production, at least for a certain period after intervention. Figure 4 shows the effect of forest management in the data of Campioli et al. Recently, Kunert et al. (2019) confirmed that disturbed forests have a higher NPP:GPP ratio in comparison with the undisturbed ones.

Variability across measurement methods

Methodological differences could account for some of the divergent results obtained in different studies. Curtis et al. (2005) compared independent methods to estimate BP and eddy covariance for GPP. Working in the transition zone between temperate deciduous and boreal forests in North America, they estimated an average NPP:GPP ratio of 0.42 ± 0.016 using biometric methods for both NPP and GPP and 0.54 ± 0.04 using biometric methods for NPP against eddy covariance GPP.

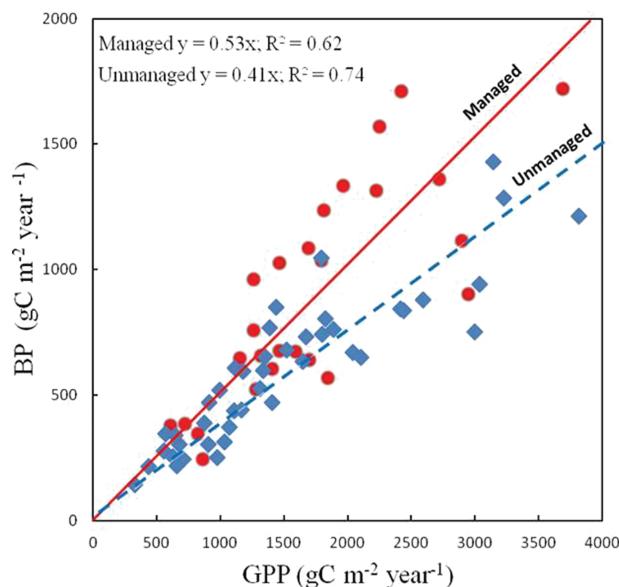


Figure 4. Regressions of BP versus GPP forced through the origin comparing managed versus unmanaged sites, from data in Campioli et al. (2015). Circles represent managed sites; squares, unmanaged sites.

By comparison with other data they suggested that the eddy covariance method was overestimating GPP at this site.

Maseyk et al. (2008) analysed the NPP:GPP ratio in a managed plantation of *Pinus halepensis* (Mill.) in Israel by comparing chamber, flux and biometric data. They also found rather large differences (up to 0.15) in annual NPP:GPP ratios estimated by the different methods (but see also Zha et al. 2007, Hermle et al. 2010; Wu et al. 2013).

Zanotelli et al. (2013), combining biometric and eddy covariance measurements for an apple orchard, found that NPP:GPP varied depending on the methodology from 0.79 ± 0.13 to 0.64 ± 0.10 . They attributed the differences to the large fraction of NPP allocated to fruit, reducing total respiration and causing higher values of the NPP:GPP ratio when compared with data reported in literature for forests.

A further potential complication in the measurement of NPP:GPP ratios, which has not been studied to our knowledge, is the possibility that CO₂ originating from sapwood respiration could be transported to and re-assimilated by the leaves. This would essentially lead to systematic underestimation of stem respiration, and thus, potentially, somewhat lower NPP:GPP ratios.

Synthesis

Despite the large number of publications since W98 that have attempted to clarify and quantify the controls on the NPP:GPP ratio, no universal picture has emerged. Different studies have come to different conclusions about the role of stand age, climate and soil fertility on this ratio (or on the ratio of BP to

GPP, in some recent works that have made the distinction). The potential role of management is a complicating factor that has only recently been recognized. The difficulty of generalization is compounded by the fact that different measurement techniques for both NPP (or BP) and GPP have been shown to yield different values. However, the range of variation in the NPP:GPP ratio appears to be substantially wider than was indicated by W98. Moreover, there are sufficient indications in the recent literature for effects of forest type (although whether due to species characteristics, climate or soil properties is unclear), stand age, site fertility and management to motivate further investigations of the controls on partitioning of GPP in forests.

Data survey

Data on annual GPP, NPP (or R_a) and NPP:GPP (or BP:GPP) ratios in forest ecosystems were compiled for this review based on previously published global data sets (e.g., De Lucia et al. 2007, Vicca et al. 2012, Tang et al. 2014, Campioli et al. 2015), supplemented by missing or more recent data from the literature (Table S1 available as Supplementary Data at *Tree Physiology Online*). NPP (or R_a) values obtained by assuming a fixed ratio to GPP were excluded from consideration. In the case of multi-year estimates, average values across years were used. Data were cross-checked to avoid repetition. The combined data set included data from 211 records for more than 100 forest stands between 5 and 500 years, with a worldwide distribution. Data collected come by diverse methodologies (e.g., eddy covariance, chamber and biometric measurements, site-level modelling) and represent different forests, which include managed and non-managed forests, mixed or pure forests, disturbed by fire or not and with different levels of soil nutrients availability at different MAT and precipitation.

The mean value for the NPP:GPP ratio in the data set is statistically indistinguishable from that given by W98, i.e., 0.46 ± 0.12 ($R^2 = 0.77, P < 0.0001, n = 211$) (Figure 5). However, specific values ranged from 0.22 (Turner et al. 2003) to 0.79 (Valentini et al. 2000), and the standard deviation was three times larger than reported by W98. Including 17 additional sets of data that included only the ratios of NPP to GPP changed the slope mean value slightly, to 0.47, but not the standard deviation ($\pm 0.12, n = 228$). Net primary production:GPP ratios by biome were $0.42 (\pm 0.12, n = 48)$ for boreal sites, $0.48 (\pm 0.12, n = 162)$ for temperate sites and $0.41 (\pm 0.11, n = 18)$ for tropical sites, thus presenting no evidence for a consistent trend with latitude and (in particular) no evidence for higher ratios of R_a :GPP in tropical sites, as might have been expected if R_a did not adapt/acclimate to temperature. However, generally higher values of the NPP:GPP ratio ($0.50 \pm 0.13, n = 71$) were shown by deciduous broad-leaf species than for evergreen needle leaf forests ($0.45 \pm 0.11, n = 12$), evergreen broad-leaf forests ($0.44 \pm 0.11, n = 127$) and mixed forests ($0.43 \pm 0.09, n = 18$). These general findings are consistent

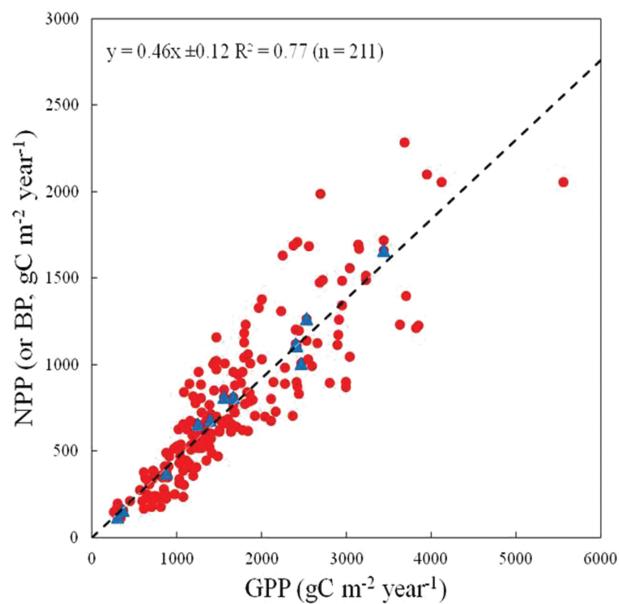


Figure 5. Regression forced through the origin ($R^2 = 0.77, P < 0.0001, n = 211$) based on the present literature survey (red dots) and data from Waring et al. (1998) (blue triangles).

with Luyssaert et al. (2007, 2009), Malhi (2012), Vicca et al. (2012) and Campioli et al. (2015), who also found that temperate deciduous forests are slightly more efficient than boreal and tropical forests in converting photosynthates into biomass. Cannell and Thornley (2000) (citing Goetz and Prince 1998) speculated that conifers might generally have smaller NPP:GPP ratios than broad-leaved species because of larger foliage biomass, which increases maintenance respiration costs but not necessarily their assimilation capacity. Values lower than 0.22 were not encountered, and it seems likely that values below 0.2 cannot be physiologically maintained (Amthor 2000; Keith et al. 2010).

What factors stabilize the NPP:GPP ratio or cause it to vary?

Twenty years on, it is now possible to answer to the question ‘Net primary production of forests: a constant fraction of gross primary production?’ (W98). Literature review has revealed that it is not. There is a compelling body of evidence that the NPP:GPP ratio is not a universal constant. However, there are mechanisms at work that tend to stabilize this ratio at a more constant value than would occur if R_a and GPP were independent. Different classes of mechanisms, tending either to stabilize or to perturb the NPP:GPP ratio, are discussed below.

The role of carbohydrate reserves

To a limited degree, plants can buffer the effects of altered carbon demand—that is, seasonal or interannual variations in R_a —by tapping into the pool of NSC (Cannell and Thornley

2000, Thornley and Cannell 2000, Trumbore 2006, Sala et al. 2012, Martínez-Vilalta et al. 2016). Over a longer time period (a few years in trees), however, increased demand for NSC to fuel increases in R_a must be reflected in reduced tissue growth (Collalti et al. 2018). This is a negative feedback mechanism, which would be expected to stabilize the NPP:GPP (Van Oijen et al. 2010), but not necessarily the BP:GPP ratio (Collalti et al. *in review*). In a purely ‘active’ view of carbon storage (i.e., storage has priority in current assimilates allocation over the structural growth; e.g., Sala et al. 2012, Collalti et al. 2016), NSC increases at the expense of BP and thus would not be accounted for, while it would be mirrored in a stepwise reduction (seasonal or for longer periods) on the NPP:GPP ratio. Conversely, in a ‘passive’ view of carbon storage (e.g., Kozlowski 1992), BP would outcompete reserve accumulation and, thus, reflecting narrower range of variations in the NPP:GPP ratio. There is mounting evidence in support of an, at least partial, active view of NSC accumulation (Dietze et al. 2014, Martínez-Vilalta et al. 2016).

W98 argued that for every mole of GPP, about half must be expended on R_a (see also Enquist et al. 2007). However, biomass produced in one year may be derived from the previous year’s photosynthates that had been allocated to NSC and subsequently remobilized and used for growth or metabolism (Gough et al. 2009, Vargas et al. 2009, Drake et al. 2016, Solly et al. 2018). Asynchrony between (photosynthetic) source and (utilization) sink implies some degree of uncoupling of R_a , and consequently NPP, from GPP. These processes are controlled in the short term by different environmental drivers: photosynthesis by light, temperature, atmospheric CO₂ concentration and water supply; respiration primarily by temperature. Noting that NSC has often been observed to increase with tree size (Sala and Hoch 2009, Richardson et al. 2013) and the potential variability of the NPP:GPP ratio due to the asynchrony of source and sink might also be expected to increase with tree size (Sala et al. 2012, Collalti et al. 2019, Collalti et al. *in review*), in contrast to the limited variability generally seen in herbaceous plants. However, how this regulation could occur at the whole-tree level is not known (Sala et al. 2012). A useful task for the future would be to compare the NPP:GPP ratio and the BP:GPP ratio across forests in different stages of development, allowing quantification of the fraction of GPP allocated to non-structural components and—we hope—contributing to an improved understanding of the regulation of the different components of the forest carbon balance.

Responses to disturbance

Plants live in a dynamic environment and are subjected to a variety of disturbances including ozone damage, fire and pest outbreaks—see, for example, the major effects of pine beetle outbreaks, as described by Edburg et al. (2011). Disturbances may force plants to deviate from homoeostasis between GPP and

R_a . The consistently higher BP:GPP ratio found by Campioli et al. (2015) for managed stands relative to unmanaged ones is likely to be attributable to thinning practices, which include the removal of suppressed and moribund trees in order to encourage the growth of younger and more efficient trees, and improve their nutrient status (see also Vanninen and Mäkelä 2005, Grant et al. 2007, Manzoni et al. 2018). More generally, it seems that any practice that leads to rejuvenation of the stands, through lowering the mean stand age and competition between individuals, may effectively tend to increase the NPP:GPP ratio (Collalti et al. 2018, Doughty et al. 2018, Kunert et al. 2019).

Changes during stand development

It is generally agreed that photosynthesis and R_a increase in parallel during early stand development. But what happens after canopy closure, when LAI stabilizes (or even slightly decreases) and GPP cannot be increased any further (Thornley and Cannell 2000)? If the NPP:GPP ratio is constant, respiration must then become constant after canopy closure (Maier et al. 2004). This is plausible for leaf respiration (and presumably also for fine root respiration), because leaf and fine root biomass are not expected to change substantially. How woody tissue respiration could remain stable, despite a continuing increase in woody biomass, is less obvious. There could be constant turnover from live to dead woody tissues, or specific respiration rates, and/or tissue nitrogen concentrations, could decrease. But there is only limited evidence that the maintenance respiration of woody biomass stabilizes (Hunt et al. 1999, Pruyne et al. 2000, Mäkelä and Valentine 2000, Vanninen and Mäkelä 2005, Grant et al. 2007, Piao et al. 2010, Goulden et al. 2011), and woody tissue respiration rates and nitrogen concentrations do not appear to change significantly (Machado and Reich 2006, Reich et al. 2008). Stem respiration may instead continue to increase, because of the continuing accumulation of sapwood biomass as trees become taller (Saxe et al. 2000; Reich et al. 2006; Mori et al. 2010), resulting in a decline in the NPP:GPP ratio over the course of stand development. Malhi (2012), Malhi et al. (2015) and Doughty et al. (2018) argued that there might be a link between high mortality rates (at least in dry tropical and more fertile sites) and high NPP:GPP ratios because of strategies in favour of inherently shorter life history and with consequent low residence time (i.e., higher turnover rates) and maintenance costs—suggesting that demographic traits might contribute to differences in NPP:GPP ratios among species.

Responses to temperature

Higher temperatures might be expected to accelerate the kinetics of all biochemical processes in plants, up to high-temperature thresholds beyond which enzymes are inactivated (Saxe et al. 2000). There is also evidence, cited also in textbooks (e.g., Larcher 2003), that the threshold temperature for inactivation of respiration is generally higher than that for

photosynthesis. So it might be inferred that the NPP:GPP ratio must decline at high temperatures. However, this reasoning overlooks the fact that the specific respiration rates of plant tissues (and the respiration rates of whole plants) acclimate to changes in temperature, so that even if the instantaneous response to temperature (driven by enzyme kinetics) remains steeply increasing (Heskel et al. 2016), the base rate changes in such a way that the rate of respiration at the new growth temperature differs little from the previous rate (Atkin and Tjoelker 2003, Gifford 2003, Medlyn et al. 2005, Smith and Dukes 2012, Atkin et al. 2015, Slot and Katajima 2015, Vanderwel et al. 2015, Reich et al. 2016). This acclimation process implies that the NPP:GPP ratio is considerably more stable with respect to growth temperature than textbook physiology would suggest. However, a comprehensive, quantitative treatment of respiratory acclimation to temperature is still missing.

Responses to soil fertility and drought

There is strong evidence that the ratio of BP to GPP varies among sites dependent on their fertility (Vicca et al. 2012, Fernández-Martínez et al. 2014), even if the mechanisms for this response are not firmly established. Across biomes, carbon allocation (below- versus above-ground) varies such that where either nutrients or water are scarce, total below-ground carbon allocation is greater (Gill and Finzi 2016). Total below-ground carbon allocation includes not only allocation to fine roots (production, respiration and turnover) but also exudation of low molecular-weight organic compounds that are unaccounted by classical measurements, which may constitute a substantial fraction (up to 30%) of NPP (Hobbie 2006, Courty et al. 2010). Vicca et al. (2012) inferred that under conditions of low nutrient availability (which can be either due to poor soils or cold climates inhibiting microbial activity) a greater fraction of assimilates are ‘lost’ through carbon transfer to root symbionts and the rhizosphere. These findings are consistent with the idea that carbon allocation follows an adaptive programme, which balances the demands of growth with the acquisition of water and nutrients required to support growth.

Conclusions

There are known mechanisms that of course couple NPP to GPP because ‘plants cannot respire what they did not photosynthesize before’ (Gifford 2003). But there is also now sufficient evidence to reject the hypothesis of a universal, constant or even tightly variable ratio of NPP to GPP, as it is used as a simplifying concept in a large number of ecosystem models. Ageing and biomass accumulation, climate, soil fertility and management have all been indicated to influence the ratio of NPP (or BP) to GPP likely in a non-mutually exclusive way. Currently available data do not allow straightforward and clear generalizations

about each of these influences: in part because of inconsistent and contrasting results among different studies, in part because of a widespread failure to distinguish NPP and BP and in part because of unresolved methodological issues affecting the measurement of NPP, R_a and GPP. The determination of whole-tree carbon budgets under different environmental conditions, at different developmental stages and even after disturbances remains a key issue for analysis. Without a clear understanding of these processes, ecosystem models are likely to continue to yield highly uncertain projections of forest carbon budgets in a changing world.

Data accessibility statement

The database used in this analysis is provided in the Supporting Information and is freely available.

Supplementary Data

Supplementary Data for this article are available at *Tree Physiology Online*.

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