Tree Physiology 00, 1–11
doi:10.1093/treephys/tpz034

Review

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

A. Collalti[1,2,6] and I.C. Prentice[3,4,5]

[1]National Research Council of Italy–Institute for Agriculture and Forestry Systems in the Mediterranean (CNR-ISAFOM), 87036, Rende, CS, Italy; [2]Foundation Euro-Mediterranean Centre on Climate Change–Impacts on Agriculture, Forests and Ecosystem Services Division (CMCC-IAFES), 01100, Viterbo, Italy; [3]Department of Life Sciences, AXA Chair of Biosphere and Climate Impacts, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, UK; [4]Department of Biological Sciences, Macquarie University, North Ryde, 2109 NSW, Australia; [5]Ministry of Education Key Laboratory for Earth System Modeling, Department of Earth System Science, Tsinghua University, Beijing 100084, China; [6]Corresponding author (alessio.collalti@isafom.cnr.it) orcid.org/0000-0002-4980-8487

Received September 24, 2018; accepted March 13, 2019; handling Editor Andrea Polle

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, CO_2 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

© The Author(s) 2019. Published by Oxford University Press. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com

Downloaded from https://academic.oup.com/treephys/advance-article-abstract/doi/10.1093/treephys/tpz034/5423351 by Max-Planck-Institut für Biogeochemie user on 22 July 2019

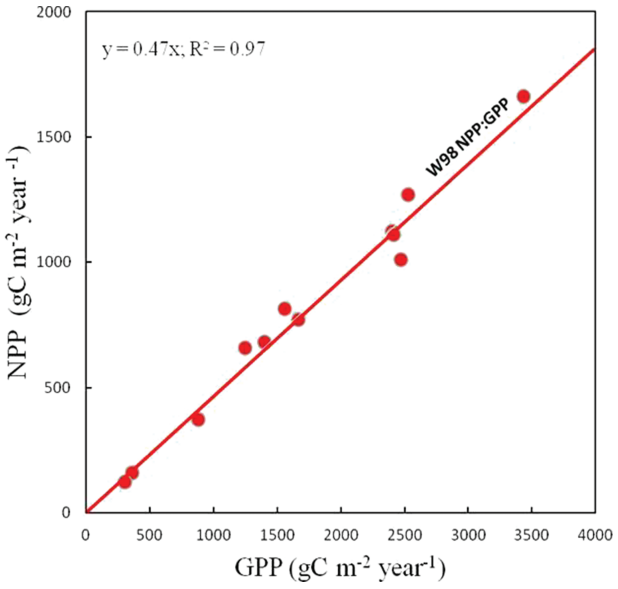

Figure 1. Regression of NPP versus GPP forced through the origin for 12 forest sites (from Waring et al. 1998, Table 2).

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 that 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 CO_2 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

Downloaded from https://academic.oup.com/treephys/advance-article-abstract/doi/10.1093/treephys/tpz034/5423351 by Max-Planck-Institut für Biogeochemie user on 22 July 2019

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 ≤ 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 CO_2 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

Downloaded from https://academic.oup.com/treephys/advance-article-abstract/doi/10.1093/treephys/tpz034/5423351 by Max-Planck-Institut für Biogeochemie user on 22 July 2019

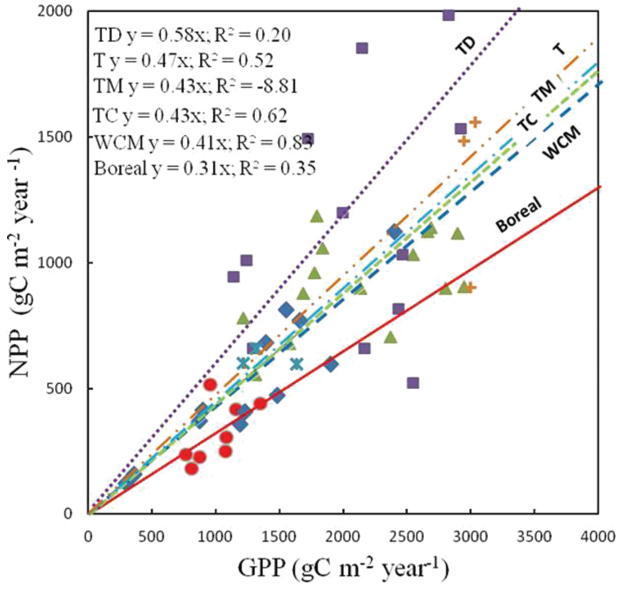

Figure 2. Regressions of NPP versus GPP forced through the origin for different forest types, from data in DeLucia et al. (2007). Circles represent boreal; squares, temperate deciduous (TD); triangles, temperate coniferous (TC); diamonds, west coast maritime (WCM); crosses, temperate mixed (TM); plus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

Downloaded from https://academic.oup.com/treephys/advance-article-abstract/doi/10.1093/treephys/tpz034/5423351 by Max-Planck-Institut für Biogeochemie user on 22 July 2019

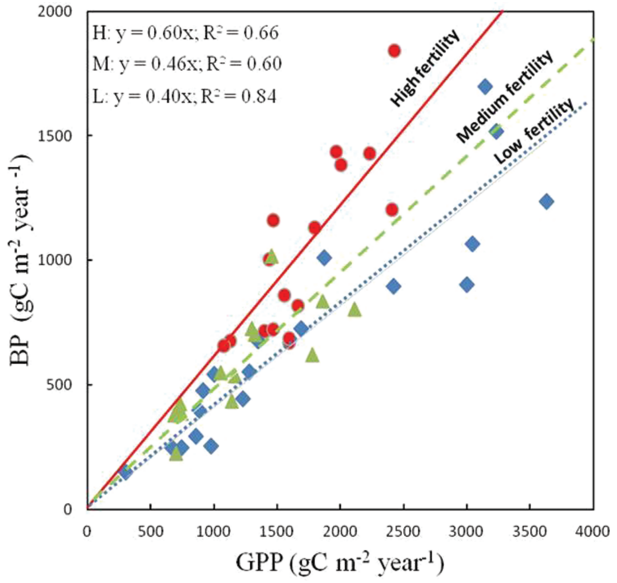

Figure 3. Regressions of BP versus GPP forced through the origin at different level of soil fertility, from data in Vicca et al. (2012). Circles, squares and triangles represent different soil nutrient availability classes, 'H', 'M' and 'L' refers to high-, medium- and low-soil fertility, respectively.

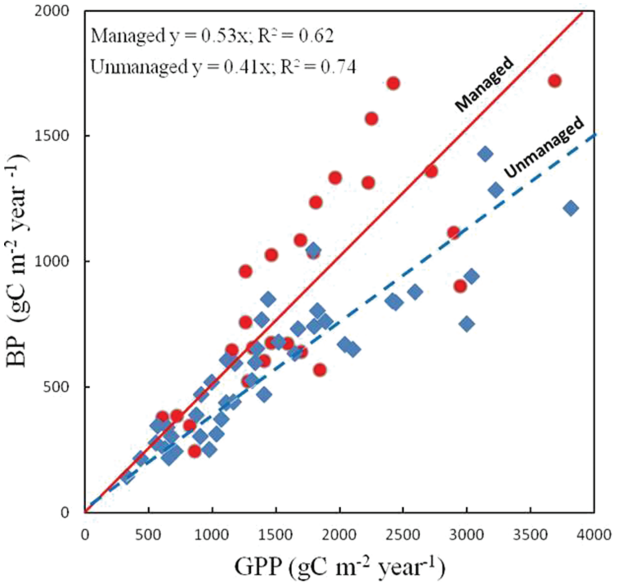

Figure 4. Regressions of BP versus GPP forced through the origin comparing managed versus unmanaged sites, from data in Campioli et al. (2015). Circles represent managed sites; squares, unmanaged sites.

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 string 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. 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 was not been studied to our knowledge, is the possibility that CO_2 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

Downloaded from https://academic.oup.com/treephys/advance-article-abstract/doi/10.1093/treephys/tpz034/5423351 by Max-Planck-Institut für Biogeochemie user on 22 July 2019

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 (± 0.12, $n = 228$). Net primary production:GPP ratios by biome were 0.42 (± 0.12, n = 48) for boreal sites, 0.48 (± 0.12, n = 162) for temperate sites and 0.41 (± 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 ± 0.13, n = 71) were shown by deciduous broad-leaf species than for evergreen needle leaf forests (0.45 ± 0.11, $n = 12$), evergreen broad-leaf forests (0.44 ± 0.11, n = 127) and mixed forests (0.43 ± 0.09, n = 18). These general findings are consistent

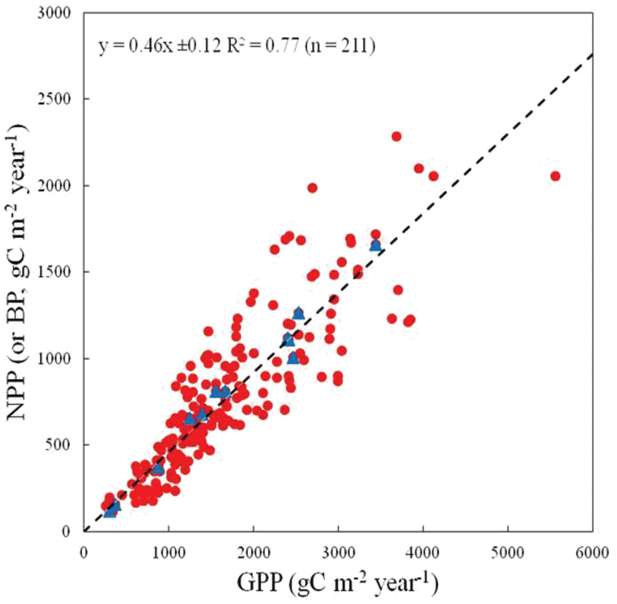

Figure 5. Regression forced through the origin ($R^2 = 0.77$, $P < 0.0001$, $n = 211$) based on the present literature survey (red dots) and data from Waring et al. (1998) (blue triangles).

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

Downloaded from https://academic.oup.com/treephys/advance-article-abstract/doi/10.1093/treephys/tpz034/5423351 by Max-Planck-Institut für Biogeochemie user on 22 July 2019

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 CO_2 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, Pruyn 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

Downloaded from https://academic.oup.com/treephys/advance-article-abstract/doi/10.1093/treephys/tpz034/5423351 by Max-Planck-Institut für Biogeochemie user on 22 July 2019

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.

Acknowledgments

We are grateful for help and invaluable assistance from A. Ibrom in conceiving and preparing the manuscript. The authors are also indebted to A. Mäkelä, G. Matteucci and B.E. Medlyn for early motivation, constructive comments and thoughtful suggestions, and to E. Grieco for data compilation and checking. We are also thankful to two anonymous reviewers for constructive comments that helped us to improve the manuscript substantially. This work is a contribution to the AXA Chair Programme in Biosphere and Climate Impacts and the Imperial College initiative on Grand Challenges in Ecosystems and the Environment (I.C.P.). I.C.P. has also received funding from the European Research Council under the European Union's Horizon 2020 research and innovation programme (grant agreement no: 787203 REALM).

References

Ågren G, Andersson F (2012) Terrestrial ecosystem ecology: principles and applications. Cambridge University Press, Cambridge, UK.

Amthor J (2000) The McCree-de wit-Penning de Vries-Thornley respiration paradigms: 30 years later. Ann Bot 86:1–20.

Atkin OA, Tjoelker MG (2003) Thermal acclimation and the dynamic response of plant respiration to temperature. TRENDS in Plant Science 8:343–351.

Atkin OA, Bloomfield KJ, Reich PB et al. (2015) Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. New Phytologist 206:614–636.

Beer C, Reichstein M, Tomelleri E et al. (2010) Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. Science 329:834–838.

Downloaded from https://academic.oup.com/treephys/advance-article-abstract/doi/10.1093/treephys/tpz034/5423351 by Max-Planck-Institut für Biogeochemie user on 22 July 2019

Campioli M, Vicca S, Luyssaert S et al. (2015) Biomass production efficiency controlled by management in temperate and boreal ecosystems. Nat Geosci 8:1–7.
Cannell M, Thornley J (2000) Modelling the components of plant respiration: some guiding principles. Ann Bot 85:45–54.
Chambers J, Tribuzy E, Toledo L et al. (2004) Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. Ecol Appl 14:72–78.
Chapin F, Woodwell G, Randerson J et al. (2006) Reconciling carbon-cycle concepts. Ecosystems 20:1041–1050.
Clark DA, Brown S, Kicklighter DW, Chambers JQ et al. (2001) Measuring net primary production in forests: concepts and field methods. Ecol Appl 11:356–370.
Collalti A, Perugini L, Santini M et al. (2014) A process-based model to simulate growth in forests with complex structure: evaluation and use of 3D-CMCC Forest ecosystem model in a deciduous forest in Central Italy. Ecol Model 272:362–378.
Collalti A, Marconi S, Ibrom A et al. (2016) Validation of 3D-CMCC Forest ecosystem model (v.5.1) against eddy covariance data for 10 European forest sites. Geosci Model Dev 9:479–504.
Collalti A, Trotta C, Keenan TF, Ibrom A, Bond-Lamberty B, Grote R et al. (2018) Thinning can reduce losses in carbon use efficiency and carbon stocks in managed forests under warmer climate. J Adv Model Earth Syst 10:2427–2452.
Collalti A, Thornton PE, Cescatti A, Rita A, Borghetti M, Nolè A, Trotta C, Ciais P, Matteucci G (2019) The sensitivity of the forest carbon budget shifts across processes along with stand development and climate change. Ecol Appl 29:1–18.
Collalti A, Tjoelker MG, Hoch G et al. Size matters: biomass accumulation and living wood turnover may dominate the uncertainty in forest autotrophic carbon balance. *New Phytol* in review.
Courty P, Buèe M, Diedhiou A et al. (2010) The role of ectomycorrhizal communities in forest ecosystem processes: new processes and emerging concepts. Soil Biol Biochem 42:679–698.
Curtis P, Vogel C, Gough C, Schmid H, Su H-B, Bovard B (2005) Respiration carbon losses and the carbon-use efficiency of a northern hardwood forest, 1999-2003. New Phytol 167:437–456.
DeLucia E, Drake J, Thomas R, Gonzalez-Meler M (2007) Forest carbon use efficiency: is a respiration a constant fraction of gross primary production? Glob Chang Biol 13:1157–1167.
Dewar RC, Medlyn BE, McMurtrie RE (1999) Acclimation of the respiration/photosynthesis ratio to temperature: insights from a model. Glob Chang Biol 5:615–622.
Dezi S, Medlyn B, Tonon G, Magnani F (2010) The effect of nitrogen deposition on forest carbon. Glob Chang Biol 16:1470–1486.
Dietze MC, Sala A, Carbone MS, Czimczik C, Mantooth JA, Richardson AD, Vargas R (2014) Nonstructural carbon in woody plants. Annual review of plant biology 65:667–687.
Doughty CE, Goldsmith GR, Raab N et al. (2018) What controls variation in carbon use efficiency among Amazonian tropical forests? Biotropica 0:1–10.
Drake JE, Gallet-Budynek A, Hofmockel KS et al. (2011) Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO_2. Ecol Lett 14:349–357.
Drake JE, Tjoelker MG, Aspinwall MJ et al. (2016) Does physiological acclimation to climate warming stabilize the ratio of canopy respiration to photosynthesis? New Phytol 211:850–863.
Edburg S, Hicke J, Lawrence D, Thornton P (2011) Simulating coupled carbon and nitrogen dynamics following. J Geophys Res 116:1–15.
Enquist BJ, Kerkhoff AJ, Huxman TE, Economo EP (2007) Adaptive differences in plant physiology and ecosystem paradoxes: insights from metabolic scaling theory. Glob Chang Biol 13:591–609.
Fernández-Martínez M, Vicca S, Janssens I et al. (2014) Nutrient availability as the key regulator of global forest carbon balance. Nat Clim Chang 4:471–476.
Galbraith D, Levy P, Sitch S et al. (2006) Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change. New Phytol 187:647–665.
Giardina C, Ryan M, Binkley D, Fownes J (2003) Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. Glob Chang Biol 9:1438–1450.
Gifford RM (1995) Whole plant respiration and photosynthesis of wheat under increased CO_2 concentration and temperature: long-term vs. short-term distinctions for modelling. Glob Chang Biol 1: 385–396.
Gifford R (2003) Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research. Funct Plant Biol 30:171–186.
Gill AL, Finzi AC (2016) Belowground carbon flux links biogeochemical cycles and resource-use efficiency at the global scale. Ecol Lett 19:1419–1428.
Girardin M, Raulier F et al. (2008) Response of tree growth to a changing climate in boreal Central Canada: a comparison of empirical, process-based, and hybrid modelling approaches. Ecol Model 213:209–228.
Goetz SJ, Prince SD (1998) Variability in carbon exchange and light utilization among boreal forest stands: implications for remote sensing and net primary production. Can J For Res 28:375–389.
Gough CM, Flower CE et al. (2009) Whole-ecosystem labile carbon production in a north temperate deciduous forest. Agric For Meteorol 149:1531–1540.
Goulden M, McMillan A, Winston G, Rocha A, Manies K, Harden J, Bond-Lamebrty B (2011) Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. Glob Chang Biol 17:855–871.
Grant RF, Barr AG, Black TA, Gaumont D et al. (2007) Net ecosystem productivity of boreal jack pine stands regenerating from clearcutting under current and future climates. Glob Chang Biol 13: 1423–1440.
Griffs T, Black T et al. (2004) Seasonal variation and partitioning of ecosystem respiration in a southern boreal aspen forest. Agric For Meteorol 125:207–223.
Heinsch F, Zhao M, Running S et al. (2006) Evaluation of remote sensing based Terrestrial productivity from MODIS using regional tower Eddy flux network observations. IEEE Trans Geosci Remote Sens 44:1908–1925.
Hermle S, Lavigne MB, Bernier PY, Bergeron O, Parè D (2010) Component respiration, ecosystem respiration and net primary production of a mature black spruce forest in northern Quebec. Tree Physiol 30:527–540.
Heskel MA, O'Sullivan O, Reich PB et al. (2016) Convergence in the temperature response of leaf respiration across biomes and plant functional types. Proc Natl Acad Sci 113:3832–3837.
Hobbie EA (2006) Carbon allocation to ectomycorrhizal fungi correlates with belowground allocation in culture studies. Ecology 87:563–569.
Huang J, Hammerbacher A, Weinhold A et al. (2018) Eyes on the future—evidence for trade-offs between growth, storage and defense in Norway spruce. New Phytol 222:144–158.
Hunt E, Lavigne M, Franklin S (1999) Factors controlling the decline of net primary production with stand age for balsam fir in Newfoundland assessed using an ecosystem simulation model. Ecol Model 122:151–164.
Ise T, Litton C et al. (2010) Comparison of modeling approaches for carbon partitioning: impact on estimates of global net primary production and equilibrium biomass of woody vegetation from MODIS GPP. J Geophys Res 115:1–11.

Downloaded from https://academic.oup.com/treephys/advance-article-abstract/doi/10.1093/treephys/tpz034/5423351 by Max-Planck-Institut für Biogeochemie user on 22 July 2019

Jay S, Potter C, Crabtree R et al. (2016) Evaluation of modelled net primary production using MODIS and landsat satellite data fusion. Carbon Balance Manag 11:1–13.

Keith H, Mackey B et al. (2010) Estimating carbon carrying capacity in natural forest ecosystems across heterogeneous landscapes: addressing sources of error. Glob Chang Biol 16:2971–2989.

Kira T, Shidei T (1967) Primary production and turnover of organic matter in different forest ecosystems of the western pacific. Jpn J Ecol 17:70–87.

Kirschbaum M (2005) A model analysis of the interaction between forest age and forest responsiveness to increasing CO2 concentration. Tree Physiol 25:953–963.

Kozlowski TT (1992) Carbohydrate sources and sinks in woody plants. Bot Rev 58:107–222.

Kunert N, El-Madany TS, Aparecido LMT, Wolf S, Potvin C (2019) Understanding the controls over forest carbon use efficiency on small spatial scales: effects of forest disturbance and tree diversity. Agric For Meteorol 269–270:136–144.

Landsberg J, Sands P (2010) Physiological ecology of forest production: principles, processes and models. Academic Press, San Diego, CA.

Landsberg J, Waring R (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For Ecol Manage 95:209–228.

Larcher W (2003) Physiological plant ecology. Springer, Berlin Heidelberg.

Lasch P, Badeck F-W, Suckow F et al. (2005) Model-based analysis of management alternatives at stand and regional level in Brandenburg (Germany). For Ecol Manage 207:59–74.

Law B, Ryan M, Anthony P (1999) Seasonal and annual respiration of a ponderosa pine ecosystem. Glob Chang Biol 5:169–182.

Lenton T, Huntingford C (2003) Global terrestrial carbon storage and uncertainties in its temperature sensitivity examined with a simple model. Glob Chang Biol 9:1333–1352.

Levy P, Cannell M, Friend A (2004) Modelling the impact of future changes in climate, CO 2 concentration and land use on natural ecosystems and the terrestrial carbon sink. Glob Environ Chang 14:21–30.

Litton C, Raich J, Ryan M (2007) Carbon allocation in forest ecosystems. Glob Chang Biol 13:2089–2109.

Luyssaert S et al. (2007) CO_2 balance of boreal, temperate and tropical forests derived from global database. Glob Chang Biol 13:2509–2537.

Luyssaert S, Reichstein M, Schulze E-D, Janssens IA, Law, BE, Papale D, Dragoni D, Goulden ML, Granier A, Kutsch WL (2009) Toward a consistency cross-check of eddy covariance flux–based and biometric estimates of ecosystem carbon balance. Global Biogeochem Cycles 23, doi: 10.1029/2008GB003377.

Machado J-L, Reich PB (2006) Dark respiration rate increases with plant size in saplings of three temperate tree species despite decreasing tissue nitrogen and nonstructural carbohydrates. Tree Physiol 26:915–923.

Magnani F, Mencuccini M, Borghetti M et al. (2007) The human footprint in the carbon cycle of temperate and boreal forests. Nature 447:848–850.

Maier C, Albaugh T et al. (2004) Respiratory carbon use and carbon storage in mid-rotation loblolly pine (*Pinus taeda* L.) plantations: the effect of site resources on the stand carbon balance. Glob Chang Biol 10:1335–1350.

Mäkelä A, Valentine H (2000) The ration of NPP to GPP: evidence of change over the course of stand development. Tree Physiol 21:1015–1030.

Malhi Y (2012) The productivity, metabolism and carbon cycle of tropical forest vegetation. J Ecol 100:65–75.

Malhi Y, Doughty C, Gabraight D (2011) The allocation of ecosystem net primary productivity in tropical forest. Philos Trans R Soc Lond B Biol Sci 366:3225–3245.

Malhi Y, Doughty CE et al. (2015) The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. Glob Chang Biol 21:2283–2295.

Malhi Y, Aragão LEOC, Metcalfe DB et al. (2009) Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. Glob Chang Biol 15:1255–1274.

Manzoni S, Čapek P, Porada P, Thurner M et al. (2018) Reviews and syntheses: carbon use efficiency from organisms to ecosystems—definitions, theories, and empirical evidence. Biogeosciences 15:5929–5949.

Martìnez-Vilalta J, Sala A, Asensio D, Galiano L, Hoch G, Palacio S, Piper FI, Lloret F (2016) Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. Ecol Monogr 86: 495–516.

Maseyk K, Grünzweig JM et al. (2008) Respiration acclimation contributes to high carbon-use efficiency in a seasonally dry pine forest. Glob Chang Biol 14:1553–1567.

McCree K (1970) An equation for the rate of respiration of white clover plants grown under controlled conditions. In: S. I. (ed) Prediction and measurement of photosynthetic productivity. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, pp 221–229.

McCree K, Troughton J (1966) Prediction of growth rate at different light levels from measured photosynthesis and respiration rates. Plant Physiol 41:559–566.

Medlyn B, Dewar R (1999) Comment on the article by R. H. Waring, J. J. Landsberg and M. Williams relating net primary production to gross primary production. Tree Physiol 19:137–138.

Medlyn BE, Robinson AP, Clement R, McMurtrie RE (2005) On the validation of models of forest CO_2 exchange using eddy covariance data: some perils and pitfalls. Tree Physiol 25:839–857.

Metcalfe D, Meir P et al. (2010) Shifts in plant respiration and carbon use efficiency at a large-scale drought experiment in the eastern Amazon. New Phytol 187:608–621.

Mori S, Yamaji K, Ishida A et al. (2010) Mixed-power scaling of whole-plant respiration from seedlings to giant trees. PNAS. doi: 10.1073/pnas.0902554107.

Nemani R, Hashimoto H et al. (2009) Monitoring and forecasting protected area ecosystem dynamics using the terrestrial observation and prediction system (TOPS). Remote Sens Environ 113:1497–1509.

Odum E (1969) The strategy of ecosystem development. Science 262–270.

Parton WJ, Hanson PJ, Swanston C, Torn M, Trumbore SE, Riley R, Kelly R (2010) ForCent model development and testing using the enriched background isotope study experiment. J Geophys Res 115:1–15.

Peichl M, Brodeur J et al. (2010) Biometric and eddy-covariance based estimates of carbon fluxes in an age-sequence of temperate pine forests. Agric For Meteorol 150:952–965.

Peng C, Liu J, Dang Q et al. (2002) TRIPLEX: a generic hybrid model for predicting forest growth and carbon and nitrogen dynamics. Ecol Model 153:109–130.

Penning de Vries F (1972) Respiration and growth. In: Rees A, Cockshull K, Hand D, Hurd R (eds) Crop processes in controlled environments. Academic Press, London, pp 327–347.

Piao S, Luyssaert S, Ciais P et al. (2010) Forest annual carbon cost: a global-scale analysis of autotrophic respiration. Ecology 91:652–661.

Pruyn M, Gartner B, Harmin M (2000) Respiratory potential in sapwood of old versus young coniferous trees. The Ecological Society of America, Washington DC, p 180.

Downloaded from https://academic.oup.com/treephys/advance-article-abstract/doi/10.1093/treephys/tpz034/5423351 by Max-Planck-Institut für Biogeochemie user on 22 July 2019

Reich PB, Tjoelker MG, Machado J-L, Oleksyn J (2006) Universal scaling of respiratory metabolism, size and nitrogen in plants. Nature 439:457–461.
Reich PB, Tjoelker MG et al. (2008) Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. Ecol Lett 11:793–801.
Reich PB et al. (2016) Boreal and temperate trees show strong acclimation of respiration to warming. Nature 531:633–636.
Richards G, Ewans D (2004) Development of a carbon accounting model (FullCAM Vers. 1.0) for the Australian continent. Aust For 67:277–283.
Richardson AD, Carbone MS et al. (2013) Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees. New Phytol 197:850–861.
Roxburgh SH, Berry SL, Buckley TN, Barnes B, Roderick ML (2005) What is NPP? Inconsistent accounting of respiratory fluxes in the definition of net primary production. Funct Ecol 19:378–382.
Ryan M (1991) Effects of climate change on plant respiration. Ecol Appl 1:157–167.
Ryan M, Gower S, Hubbard R et al. (1995) Woody tissue maintenance respiration of four conifers in contrasting climate. Oecologia 110:133–140.
Ryan M, Binkley D, Fowners J (1997*a*) Age-related decline in forest productivity: pattern and process. Adv Ecol Res 27:213–262.
Ryan M, Lavigne M, Gower S (1997*b*) Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. J Geophys Res 102:871–884.
Ryan M, Binkley D, Fownes J, Giardina C, Senock R (2004) An experimental test of the causes of forest growth decline with stand age. Ecol Monogr 74:393–414.
Ryan M, Philips N, Bond B (2006) The hydraulic limitation hypothesis revisited. Plant Cell Environ 29:367–381.
Sala A, Hoch G (2009) Height-related growth declines in ponderosa pine are not due to carbon limitation. Plant Cell Environ 32:22–30.
Sala A, Woodruff DR, Meinzer FC (2012) Carbon dynamics in trees: feast or famine? Tree Physiol 32:764–775.
Sands P, Battaglia M, Mummery D (2000) Application of process-based models to forest management: experience with PROMOD, a simple plantation productivity model. Tree Physiol 20:383–392.
Saxe H, Cannell M et al. (2000) Tree and forest functioning in response to global warming. New Phytol 149:369–400.
Seidl R, Rammer W, Scheller R, Spies T (2012) An individual-based process model to simulate landscape-scale forest ecosystem dynamics. Ecol Model 213:87–100.
Slot M, Katajima K (2015) General patterns of acclimation of leaf respiration to elevated temperatures across biomes and plant types. Oecologia 177:885–900.
Smith N, Dukes J (2012) Plant respiration and photosynthesis in a global-scale models: incorporating acclimation to temperature and CO_2. Glob Chang Biol 19:1–19.
Solly EF, Brunner I, Helmisaari H-S, Herzog C, Leppälammi-Kujansuu J, Schöning I, Schrumpf M, Schweingruber FH, Trumbore SE, Hagedorn F (2018) Unravelling the age of fine roots of temperate and boreal forests. Nat Commun 9:1–8.
Sun Y, Gu L et al. (2014) Impact of mesophyll diffusion on estimated global land CO2 fertilization. Proc Natl Acad Sci USA 111:15774–15779.
Tang J, Luyssaert S, Richardson A et al. (2014) Steeper declines in forest photosynthesis that respiration explain age-driven decreases in forest growth. Proc Natl Acad Sci USA 111:8856–8860.
Thornley J (1970) Respiration, growth and maintenance in plants. Nature 227:304–305.
Thornley J (2011) Plant growth and respiration re-visited: maintenance respiration defined it is an emergent property of, not a separate process within, the system and why the respiration: photosynthesis ratio is conservative. Ann Bot 108:1365–1380.
Thornley JH, Cannell M (2000) Modelling the components of plant respiration: representation and realism. Ann Bot 85:55–67.
Tjoelker M, Oleskyn J, Reich P (1999) Acclimation of respiration to temperature and CO_2 in seedlings of boreal tree species in relation to plant size and relative growth rate. Glob Chang Biol 49:679–691.
Trumbore S (2006) Carbon respired by terrestrial ecosystems—recent progress and challenges. Glob Chang Biol 12:141–153.
Turner D, Ritts W, Cohen W et al. (2003) Scaling gross primary production (GPP) over boreal and deciduous forest landscape in support of MODIS GPP product validation. Remote Sens Environ 88:256–270.
Valentini R, Matteucci G, Dolman AJ, Schulze ED, Rebmann C, Moors EJ et al. (2000) Respiration as the main determinant of carbon balance in European forests. Nature 404:861–865.
Vargas R, Trumbore SE, Allen MF (2009) Evidence of old carbon used to grow new fine roots in a tropical forest. New Phytol 182:710–718.
Vanderwel MC, Slot M, Lichstein JW, Reich PB, Kattge J, Atkin OK, Bloomfield KJ (2015) Global convergence in leaf respiration from estimates of thermal acclimation across time and space. New Phytol 207:1026–1037.
Van Oijen M, Rougier J, Smith R (2005) Bayesian calibration of process-based models: bridging the gap between models and data. Tree Physiol 25:915–927.
Van Oijen M, Schapendonk A, Hoglind M (2010) On the relative magnitudes of photosynthesis, respiration, growth and carbon storage in vegetation. Ann Bot 105:739–797.
Vanninen P, Mäkelä A (2005) Carbon budget for scots pine trees: effects of size, competition and site fertility on growth allocation and production. Tree Physiol 25:17–30.
Veroustraete F, Sabbe H, Eerens H (2002) Estimation of carbon mass fluxes over Europe using C-fix model and Euroflux data. Remote Sens Environ 83:376–399.
Vicca S, Luyssaert S et al. (2012) Fertile forests produce biomass more efficiently. Ecol Lett 15:520–526.
Waring R, Landsberg JL (2016) Tamm review: insights gained from light use and leaf growth efficiency. For Ecol Manage 379:232–242.
Waring RH, Landsberg J, Williams M (1998) Net primary production of forests: a constant fraction of gross primary production? Tree Physiol 18:129–134.
Wohlfahrt G, Lu L (2015) The many meanings of gross photosynthesis and their implication for photosynthesis research from leaf to globe. Plant Cell Environ 38:2500–2507.
Wu J, Larsen K, van der, Linden L, Beier C, Pileegard K, Ibrom A (2013) Synthesis on the carbon budget and cycling in a Danish, temperate deciduous forest. Agric For Meteorol 181:94–107.
Zanotelli D, Montagnani L, Manca G, Tagliavini M (2013) Net primary productivity, allocation pattern and carbon use efficiency in an apple orchard assessed by integrating eddy covariance, biometric and continuous chamber measurements. Biogeosciences 10:3089–3108.
Zha T, Xing Z, Wang K-Y, Kellomäki S, Barr AG (2007) Total and component carbon fluxes of a scots pine ecosystem from chamber measurement and Eddy covariance. Ann Bot 99:345–353.
Zha T, Barr AG, Black A et al. (2009) Carbon sequestration in boreal jack pine stands following harvesting. Glob Chang Biol 15:1475–1487.
Zhang J-H, Han S-J et al. (2006) Seasonal variation in carbon dioxide exchange over a 200-year-old Chinese broad-leaved Korean pine mixed forest. Agric For Meteorol 137:150–165.
Zhang Y, Yu G, Yang J, Wimberly MC, Zhang XC, Tao J, Jiang Y, Zhu J (2013) Climate-driven global changes in carbon use efficiency. Glob Ecol Biogeogr 23:144–155.

Downloaded from https://academic.oup.com/treephys/advance-article-abstract/doi/10.1093/treephys/tpz034/5423351 by Max-Planck-Institut für Biogeochemie user on 22 July 2019