

Comparison of modeling approaches for carbon partitioning: Impact on estimates of global net primary production and equilibrium biomass of woody vegetation from MODIS GPP

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[1] Partitioning of gross primary production (GPP) to aboveground versus belowground, to growth versus respiration, and to short versus long-lived tissues exerts a strong influence on ecosystem structure and function, with potentially large implications for the global carbon budget. A recent meta-analysis of forest ecosystems suggests that carbon partitioning to leaves, stems, and roots varies consistently with GPP and that the ratio of net primary production (NPP) to GPP is conservative across environmental gradients. To examine influences of carbon partitioning schemes employed by global ecosystem models, we used this meta-analysis-based model and a satellite-based (MODIS) terrestrial GPP data set to estimate global woody NPP and equilibrium biomass, and then compared it to two process-based ecosystem models (Biome-BGC and VISIT) using the same GPP data set. We hypothesized that different carbon partitioning schemes would result in large differences in global estimates of woody NPP and equilibrium biomass. Woody NPP estimated by Biome-BGC and VISIT was 25% and 29% higher than the meta-analysis-based model for boreal forests, with smaller differences in temperate and tropics. Global equilibrium woody biomass, calculated from model-specific NPP estimates and a single set of tissue turnover rates, was 48 and 226 Pg C higher for Biome-BGC and VISIT compared to the meta-analysis-based model, reflecting differences in carbon partitioning to structural versus metabolically active tissues. In summary, we found that different carbon partitioning schemes resulted in large variations in estimates of global woody carbon flux and storage, indicating that stand-level controls on carbon partitioning are not yet accurately represented in ecosystem models.

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1. Introduction

[2] The partitioning of assimilated carbon from gross primary production (GPP) by woody plants into leaf, stem, and root tissues has a strong impact on the carbon balance and life strategy of individual plants [Johnson and Thornley, 1987], ecosystem structure and functioning [Ryan, 1991; Ryan *et al.*, 2004; Litton *et al.*, 2007; Litton and Giardina, 2008], and, ultimately, global terrestrial carbon cycling [Friedlingstein *et al.*, 1999]. The plasticity of carbon partitioning (carbon flux as a fraction of GPP; Figure 1) provides

a mechanism for plants to improve resource acquisition in an environment where multiple aboveground and belowground resources can simultaneously limit plant production [Iwasa and Roughgarden, 1984]. Moreover, the ratio between NPP and GPP, carbon use efficiency, plays an important role in controlling forest carbon balance [DeLucia *et al.*, 2007; Litton *et al.*, 2007; Zhang *et al.*, 2009]. Across larger scales, shifts in partitioning by plants exert a large influence on regional and global carbon balance, but our understanding of how this balance will respond to changes in climate, and corresponding assumptions driving partitioning schemes in ecosystem models, remain poorly constrained.

[3] Ecosystems dominated by woody vegetation are responsible for 69–76% of global NPP and 77–82% of carbon storage in plant biomass (calculated from Prentice *et al.* [2001]). Given the large influence of woody biomes on the global carbon cycle, an accurate understanding of carbon partitioning in woody ecosystems is essential for modeling the potential impact of environmental change on the terrestrial carbon balance. For example, based on a resource optimization theory [Iwasa and Roughgarden, 1984],

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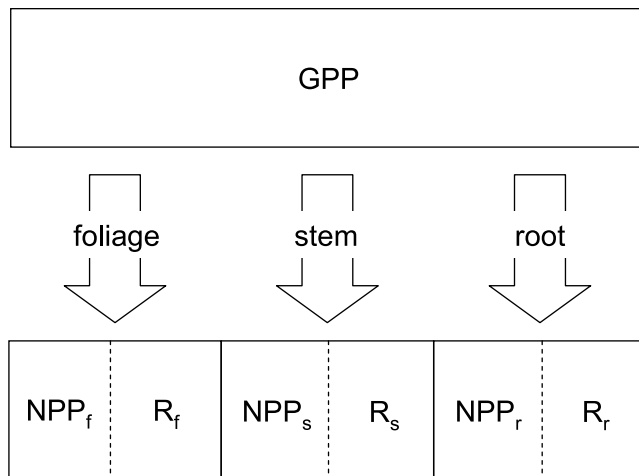


Figure 1. Schematic diagram of the partitioning of GPP in terrestrial ecosystems (modified from *Ryan* [1991]). GPP is allocated to six fluxes: NPP and autotrophic respiration of foliage, stems, and roots (NPP_f , R_f , NPP_s , R_s , NPP_r , and R_r).

Friedlingstein et al. [1999] modified carbon partitioning to woody plant tissues (shoot versus root) as a dynamic function of resource availability and demonstrated that the subsequent global estimate of plant biomass was reduced by 10% when compared to a fixed partitioning scheme. However, despite the important role of carbon partitioning in ecosystem carbon balance, a unified theory describing carbon partitioning and the underlying empirical framework are conspicuously lacking [*Reynolds and Chen*, 1996; *Enquist and Niklas*, 2002; *DeLucia et al.*, 2007; *Litton et al.*, 2007]. As a result, model treatment of carbon partitioning has potentially large implications for regional and global estimates of carbon flux and storage.

[4] From a meta-analysis of 63 field studies ranging from tropical wet to boreal forests, *Litton et al.* [2007] reviewed and analyzed carbon partitioning in forest ecosystems, referred to here as the “meta-analysis-based partitioning scheme.” This analysis predicts constant partitioning of GPP to foliage (0.26 ± 0.03 SE; SE calculated from the meta-analysis data set, $n = 29$), while partitioning of GPP to stems increases linearly with GPP and partitioning to roots decreases linearly with GPP. The meta-analysis-based partitioning scheme also predicts that stand carbon use efficiency, defined as the ratio between NPP and GPP, is constant across a wide range of forest types (mean ecosystem carbon use efficiency of 0.43 ± 0.02 SE; $n = 23$). The meta-analysis-based partitioning scheme also identified that carbon use efficiency does vary by component with carbon use efficiencies of $0.36 (\pm 0.02$ SE), $0.60 (\pm 0.03$ SE), and $0.41 (\pm 0.03$ SE) for foliage, stems (aboveground metabolically active and inactive woody tissues), and roots (coarse and fine roots), respectively. Critically, these values represent central tendencies; for yet to be determined reasons, variation within and across sites can be quite high. For example, stand carbon use efficiency varied from 0.29 to 0.58 across all studies analyzed by *Litton et al.* [2007], in line with findings of *Amthor* [2000], who reported that the potential range of carbon use efficiency is 0.20–0.65 in individual plants over long periods.

[5] Global vegetation models are widely used to study interactions between terrestrial ecosystems and global change [*Moorcroft*, 2006]. For example, vegetation models are regularly coupled to general circulation models [e.g., *Cox et al.*, 2000; *Kawamiya et al.*, 2005] to reproduce land-atmosphere feedbacks in biogeochemistry (e.g., carbon cycling dynamics) and biophysics (e.g., albedo and hydrological cycles). Despite the effects of carbon partitioning algorithms on model output, only *Friedlingstein et al.* [1999] has systematically studied the impacts of partitioning scheme on a global terrestrial ecosystem model. Since many models calculate maintenance and growth respiration separately [*Ryan*, 1990] and assume positive temperature sensitivity for respiration rates, modification of these processes by the meta-analysis-based partitioning scheme has the potential to significantly alter estimates of carbon storage and flux by terrestrial vegetation models.

[6] The first objective of this study was to estimate woody plant NPP and equilibrium biomass (where NPP and tissue turnover equilibrate) using the meta-analysis-based partitioning scheme applied to a MODIS-derived global GPP data set [*Running et al.*, 2004]. Our second objective was to compare woody NPP and equilibrium biomass from this approach with two widely used process-based models: Biome-BGC [*Running and Hunt*, 1993; *Running et al.*, 2004; *Zhao et al.*, 2005] and VISIT [*Ito and Oikawa*, 2002; *Ito*, 2005]. Our goal in this comparison was to test whether differences in model treatment of carbon partitioning significantly impact estimates of global carbon flux and storage in live woody biomass. We hypothesized that different model treatments of carbon partitioning would result in large differences in global estimates of woody NPP and equilibrium biomass. Since all three approaches relied on the same GPP data set to estimate NPP and equilibrium biomass, any observed differences would be a direct consequence of the different carbon partitioning algorithms employed. We also explored how carbon use efficiency (NPP:GPP) estimates vary across the different modeling approaches, and how this variation, along with component-specific (foliage, stem, and roots) efficiencies, impacts global equilibrium woody biomass estimates.

2. Materials and Methods

[7] Global GPP was obtained from the MODIS (MOD17) database, and woody plant NPP was then estimated with the three different carbon partitioning algorithms (meta-analysis-based partitioning scheme, Biome-BGC, and VISIT). Both Biome-BGC and VISIT rely on constant fractions to partition GPP into foliage, stem, and roots (Tables 1 and 2). In the meta-analysis-based partitioning scheme approach, however, only partitioning to foliage is a constant fraction of GPP, while partitioning to stem and roots varies linearly with GPP [*Litton et al.*, 2007]. Partitioning to production versus respiration also varies across the three models. Biome-BGC and VISIT calculate carbon use efficiency based on temperature and biomass, while the meta-analysis-based partitioning scheme approach estimates partitioning of GPP to respiration based on component-specific constants (carbon use efficiencies of 0.36, 0.60, and 0.41 for foliage, stems, and roots, respectively). Once partitioning to component tissues and production versus respiration has been quantified in each model, the global distribution of equilibrium woody biomass

Table 1. Carbon Partitioning Parameters and Tissue Turnover Rates Summarized From VISIT

Parameter	Symbol	Unit	Tropical Forest	Temperate Forest	Boreal Forest	Sparse Woodland
Foliage maintenance respiration	k_{mf}	yr^{-1}	1.40×10^0	1.38×10^0	1.25×10^0	1.40×10^0
Stem sapwood maintenance respiration	k_{mss}	yr^{-1}	5.30×10^{-2}	5.55×10^{-2}	5.04×10^{-2}	7.05×10^{-2}
Root sapwood maintenance respiration	k_{mrs}	yr^{-1}	2.07×10^{-1}	2.28×10^{-1}	2.06×10^{-1}	3.57×10^{-1}
Stem heartwood maintenance respiration	k_{msh}	yr^{-1}	2.57×10^{-3}	3.50×10^{-3}	3.18×10^{-3}	6.37×10^{-3}
Root heartwood maintenance respiration	k_{mrh}	yr^{-1}	1.47×10^{-2}	1.78×10^{-2}	1.52×10^{-2}	3.02×10^{-2}
Partitioning to foliage	f_f^a	fraction of carbon surplus	0.193	0.198	0.134	0.235
Partitioning to stem (see Appendix A)	f_s^a	fraction of carbon surplus	0.517	0.500	0.500	0.232
Foliage growth respiration	k_{gf}	fraction of carbon surplus	0.500	0.498	0.466	0.505
Stem growth respiration	k_{gs}	fraction of carbon surplus	0.127	0.145	0.118	0.187
Root growth respiration	k_{gr}	fraction of carbon surplus	0.227	0.243	0.214	0.282
Foliage tissue turnover	t_f	yr^{-1}	1.33	1.08	0.702	0.904
Stem tissue turnover	t_s	yr^{-1}	0.0342	0.0234	0.0108	0.0342
Root tissue turnover	t_r	yr^{-1}	0.385	0.288	0.137	0.385

^aPartitioning to roots (f_r) is calculated as a residual term in VISIT (i.e., any carbon left over after partitioning to leaves and stems goes to roots).

is estimated from model output of NPP and a data set of plant tissue turnover rates from VISIT. Importantly, the same woody plant GPP and plant tissue turnover rates were used in each model run, such that differences in model estimates of global woody NPP and equilibrium biomass are a direct consequence of model-specific carbon partitioning schemes.

2.1. GPP From MODIS

[8] The MODIS GPP (MOD17 for 2001–2006, ~ 1 km resolution, 8 day mean [Running *et al.*, 2004; Zhao *et al.*, 2005; Turner *et al.*, 2006]) was obtained from LP DAAC (<http://edcdaac.usgs.gov/>). This is an 8 day composite at 1 km spatial resolution in validated stage 3 (very low commission error) that employs a linear temporal gap-filling technique to replace missing data. Annual GPP was simply calculated by aggregating the 8 day means. The original data set in a ~ 1 km sinusoidal projection was converted into the 0.5° Mercator projection (Figure 2). The GPP estimate by MODIS comes from a simple empirical model that is a function of the fraction of photosynthetically active radiation absorbed by vegetation, leaf area index (obtained from MOD15A2 [Knyazikhin *et al.*, 1998, 1999]), vapor pressure deficit, and daily minimum air temperature. The mean GPP reported here ($76.3 \text{ Pg C yr}^{-1}$ for 2001–2006) is only for biomes dominated by woody vegetation, and thus it is $\sim 30\%$ lower than that estimated for all terrestrial vegetation reported by Zhao *et al.* [2005] (109 Pg C yr^{-1} for the mean of 2001–2003). We do not contend that this global GPP data set represents an improvement over other global estimates, but rather use this data set to address our objectives of modeling carbon partitioning, flux and storage from a single GPP data set. Thus, this global data set of MODIS-derived GPP was used in each of the three models to calculate global woody NPP and equilibrium biomass on the same 0.5° grid.

2.2. Global Woody NPP

[9] Both process-based models (Biome-BGC and VISIT) calculate maintenance and growth respiration terms separately, while the meta-analysis-based partitioning scheme directly estimates total autotrophic respiration based on statistical relationships from the meta-analysis presented by Litton *et al.* [2007]. The process-based models calculate respiration as functions of tissue biomass and temperature with fixed carbon partitioning coefficients. In contrast, Litton *et al.* [2007] found that for forest ecosystems, carbon parti-

tioning is not well correlated with living biomass and, thus, the meta-analysis-based partitioning scheme calculates respiration by tissue component as a direct proportion of GPP based on a synthesis of empirical relationships developed for diverse forest sites (see section 4).

[10] The meta-analysis-based partitioning scheme uses statistical relationships to partition GPP into 3 biomass compartments (foliage, stem, and roots), and then calculates NPP versus autotrophic respiration separately for each compartment. Annual woody GPP ($\text{g C m}^{-2} \text{ yr}^{-1}$) partitioning to foliage (GPP_f), stem (GPP_s), and root (GPP_r) components was calculated from total GPP ($\text{g C m}^{-2} \text{ yr}^{-1}$) determined from MODIS as:

$$GPP_f = 0.258 \times GPP \quad (1)$$

$$GPP_s = (c_s \times GPP + c_i) \times GPP \quad (2)$$

$$GPP_r = (-c_s \times GPP + 1 - 0.258 - c_i) \times GPP \quad (3)$$

where $c_s = 5.06 \times 10^{-5}$ and $c_i = 0.194$. As shown here, partitioning of annual woody GPP to stem versus roots is a function of GPP, while partitioning to foliage is constant. NPP ($\text{g C m}^{-2} \text{ yr}^{-1}$) for foliage (NPP_f), stem (NPP_s), and roots (NPP_r) was calculated from GPP_f , GPP_s , and GPP_r , respectively, with component-specific carbon use efficiency constants:

$$NPP_f = 0.360 \times GPP_f \quad (4)$$

$$NPP_s = 0.589 \times GPP_s \quad (5)$$

$$NPP_r = 0.410 \times GPP_r \quad (6)$$

[11] Biome-BGC [Running and Hunt, 1993; White *et al.*, 2000; Running *et al.*, 2004; Zhao *et al.*, 2005] is a widely

Table 2. Carbon Partitioning Coefficients for Biome-BGC, Calculated From White *et al.* [2000], Which Assumes Constant Partitioning of Carbon to Leaves, Stems, and Roots That Vary With Forest Type

Partitioning Fractions	Evergreen Needleleaf Forest	Deciduous Needleleaf Forest	Deciduous Broadleaf Forest	Shrubland	Evergreen Broadleaf Forest
Leaf	0.19	0.21	0.20	0.44	0.30
Stem	0.42	0.47	0.45	0.10	0.30
Root	0.39	0.32	0.34	0.47	0.39

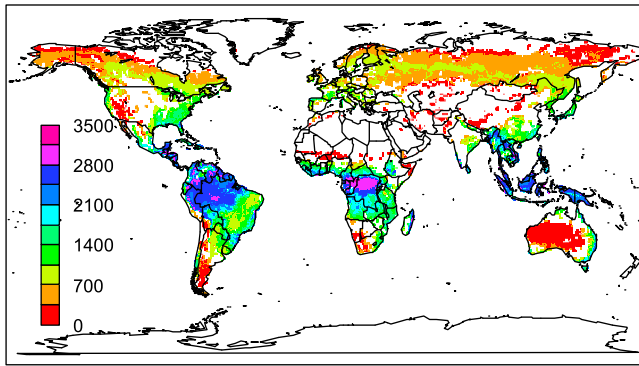


Figure 2. Global woody plant GPP ($\text{g C m}^{-2} \text{ yr}^{-1}$) from MODIS (mean of 2001–2006).

used ecosystem model that simulates ecophysiological processes of vegetation and soil biogeochemical cycles. Partitioning of GPP into plant tissues is based on partitioning constants that vary with vegetation type (Table 2). NPP estimated by Biome-BGC is calculated by subtracting maintenance and growth respiration from GPP that is simulated by a Farquhar-type ecophysiological model. Maintenance respiration has a temperature dependency ($Q_{10} = 2.0$), and growth respiration is a constant fraction of carbon partitioned to each component. Details of the Biome-BGC NPP calculation are given by *Running and Coughlan [1988]*, *Running and Gower [1991]*, and *Zhao et al. [2005]*. The NPP product calculated by Biome-BGC is distributed as a part of the MOD17 product. The annual NPP data set (2001–2006) is available from <http://www.ntsg.umt.edu/modis/>.

[12] VISIT [*Ito, 2005*] is based on the ecosystem model Sim-CYCLE [*Ito and Oikawa, 2002*] and has vegetation ecophysiology submodels and ecosystem models of plant production and soil biogeochemistry. Partitioning of GPP into plant tissues is based on partitioning constants that vary with vegetation type (Table 1). VISIT estimates maintenance respiration and growth respiration of foliage, stem, and roots separately. The maintenance respiration is proportional to biomass and also has a dependence on temperature ($Q_{10} = 2.2$ at 5°C , $Q_{10} = 2.0$ at 15°C , and $Q_{10} = 1.8$ at 25°C), taking into account size dependence (i.e., sapwood/heartwood ratio) and temperature acclimation. Growth respiration of each tissue (i.e., foliage, stem, and roots) is a constant fraction of partitioned carbon (Table 1). A set of simplified equations from the original VISIT was applied to this study (see Appendix A) to estimate partitioning to respiration for NPP estimates.

2.3. Global Equilibrium Woody Biomass

[13] Equilibrium biomass of woody plants from each model was calculated based on model-specific NPP estimates and a simple tissue turnover model employed by VISIT (Table 1). The use of a single calculation algorithm to obtain the equilibrium biomass from the NPP output for each model allowed us to explore how the carbon partitioning scheme for each model impacts terrestrial carbon storage in live biomass. VISIT assigns vegetation-specific turnover rates for foliage, stems, and roots (Table 1). The vegetation type of each grid cell was obtained from an existing global vegetation map [*Hansen et al., 1998*], and the grid was then assigned to the

most closely corresponding biome type used in VISIT. From 13 land cover types of GLCF UMD Global Land Cover Classification [*Hansen et al., 1998*], we summarized woody vegetation into 3 categories: (1) tropical and subtropical forest, (2) moist temperate forest and second-growth forest following anthropogenic land use, and (3) boreal forest. These categories included open woodlands such as semiarid woodland and savanna. The amounts of equilibrium biomass in foliage, stem, and roots (C_{ef} , C_{es} , and C_{er} , respectively) were calculated by solving the following differential equations for equilibria:

$$\frac{dC_f}{dt} = NPP_f - k_f \cdot C_f \quad (7)$$

$$\frac{dC_s}{dt} = NPP_s - k_s \cdot C_s \quad (8)$$

$$\frac{dC_r}{dt} = NPP_r - k_r \cdot C_r \quad (9)$$

and gives:

$$C_{ef} = \frac{NPP_f}{k_f} \quad (10)$$

$$C_{es} = \frac{NPP_s}{k_s} \quad (11)$$

$$C_{er} = \frac{NPP_r}{k_r} \quad (12)$$

where k_f , k_s , and k_r are tissue turnover rates of foliage, stem, and roots, respectively, that are constant through time but vary by biome (Table 1). We assumed no internal variability in tissue turnover rates in each vegetation type.

2.4. Sensitivity Analysis

[14] To understand the sensitivity of modeled NPP and equilibrium biomass to partitioning assumptions, we conducted a sensitivity analysis of carbon partitioning parameters for the meta-analysis-based partitioning scheme by systematically varying c_i (“intercept” parameter in equations (2) and (3)) for all modeled forest types. From the default value of the meta-analysis-based partitioning scheme ($c_i = 0.194$), c_i was either increased or reduced by 20% to vary stem to root partitioning. Since stem and roots have different carbon use efficiency and tissue turnover time, the resultant NPP and equilibrium biomass are also affected. In addition, c_s (“slope” parameter) was also changed by doubling ($c_s = 1.01 \times 10^{-4}$) and zeroing c_s ($c_s = 0$) to explore the effect of productivity (GPP) on stem to root partitioning.

3. Results

[15] Because a single GPP data set was used for all three modeling analyses, the three analyses reproduced similar large-scale patterns in NPP including a strong latitudinal gradient in NPP (Figure 3) with the highest NPP values in moist tropical regions. However, model-specific differences were also apparent for many regions. For example, the meta-analysis-based model estimated higher NPP for the Amazon

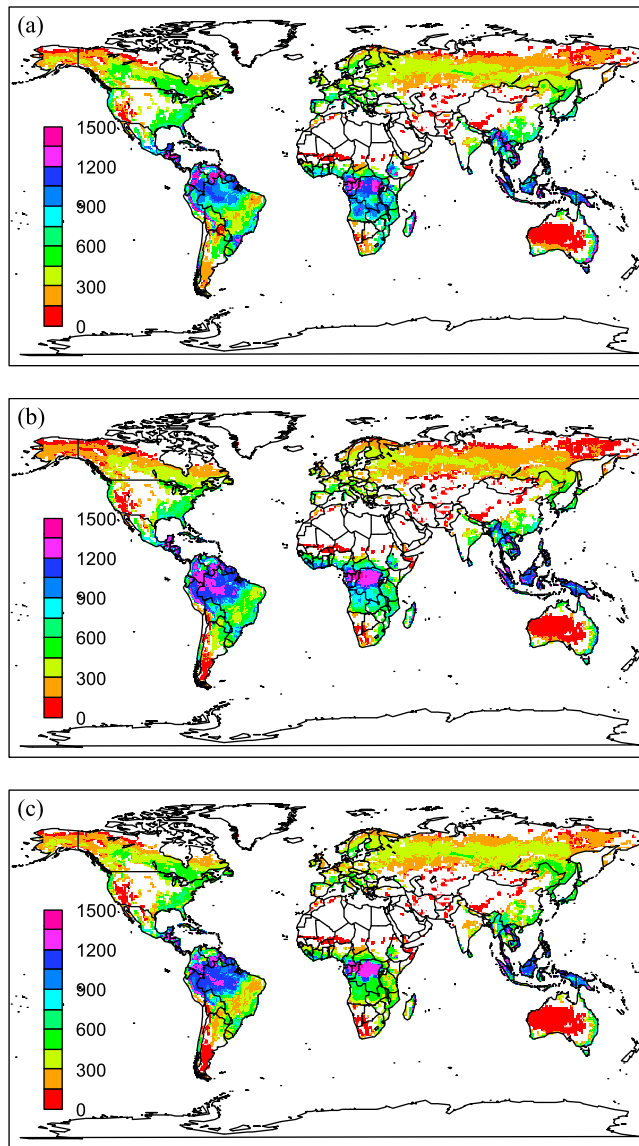


Figure 3. Global woody plant NPP ($\text{g C m}^{-2} \text{yr}^{-1}$) from (a) Biome-BGC, (b) the meta-analysis-based partitioning scheme, and (c) VISIT (mean of 2001–2006).

basin than the process-based models (lower modeled respiration costs compared to Biome-BGC and VISIT). On the other hand, boreal forest productivity, especially in Canada, was lower in the meta-analysis-based scheme (higher modeled respiration costs).

[16] Within a given biome, estimates of NPP differed significantly across models (Table 3). Due to the temperature sensitivity of maintenance respiration, the process-based models (Biome-BGC and VISIT) estimated NPP in boreal forests to be 25% and 29% higher, respectively, than the meta-analysis-based partitioning scheme ($p < 0.01$, Tukey's HSD). Model NPP estimates from VISIT agreed well with the meta-analysis-based partitioning scheme for temperate and tropical forests. However, Biome-BGC estimates of global woody NPP were 6–8% lower in tropical forests and 16% higher in temperate forests compared to the other two models.

[17] Since the temperature dependence of maintenance respiration lowered carbon loss in cold regions (see equation (A1) in Appendix A), it also reduced the latitudinal gradient of NPP predicted by the process-based models (Figure 4). On the other hand, NPP estimated by the meta-analysis-based partitioning scheme reflected the latitudinal gradient of GPP directly. Moreover, NPP estimated with Biome-BGC for tropical wet forests in the Amazon and central Africa tended to be lower than the other two models but was higher in savanna and subtropical regions (Figure 4), likely because the temperature sensitivity of respiration in Biome-BGC was the highest among the models.

[18] Different carbon partitioning schemes employed by the three models affected global equilibrium woody biomass estimates (Table 3 and Figure 5). VISIT had higher estimates than the meta-analysis-based partitioning scheme and Biome-BGC in tropical forests by 27% and 41%, respectively (Figure 6). In temperate and boreal forests, the meta-analysis-based partitioning scheme had significantly lower biomass estimates than the process-based models ($p < 0.01$), while that of VISIT was significantly higher than Biome-BGC in both regions ($p < 0.01$). Importantly, differences in estimates of biomass originated solely from the different carbon partitioning schemes employed by each model. For example, greater partitioning to stems, which have a lower tissue turnover rate (Table 1), will result in larger equilibrium biomass. Across cover types, the meta-analysis-based

Table 3. Summary Output of Gross Primary Productivity, Net Primary Productivity, and Equilibrium Biomass for Global Woody Vegetation^a

Variable	Region	Unit	Biome-BGC	Meta-Analysis	VISIT
GPP	tropical	$\text{g C m}^{-2} \text{yr}^{-1}$	2113 ± 27	2113 ± 27	2113 ± 27
	temperate	$\text{g C m}^{-2} \text{yr}^{-1}$	899 ± 11	899 ± 11	899 ± 11
	boreal	$\text{g C m}^{-2} \text{yr}^{-1}$	550 ± 17	550 ± 17	550 ± 17
	woody biome total	Pg C yr^{-1}	108.7 ± 1.3	108.7 ± 1.3	108.7 ± 1.3
NPP	tropical	$\text{g C m}^{-2} \text{yr}^{-1}$	870 ± 28 (a)	950 ± 27 (b)	928 ± 13 (b)
	temperate	$\text{g C m}^{-2} \text{yr}^{-1}$	455 ± 8 (a)	393 ± 5 (b)	392 ± 5 (b)
	boreal	$\text{g C m}^{-2} \text{yr}^{-1}$	297 ± 11 (a)	238 ± 7 (b)	308 ± 10 (a)
	woody biome total	Pg C yr^{-1}	50.5 ± 1.1 (a)	48.1 ± 0.6 (b)	43.8 ± 0.5 (c)
Equilibrium biomass	tropical	kg C m^{-2}	11.6 ± 0.4 (a)	12.8 ± 0.2 (b)	16.3 ± 0.2 (c)
	temperate	kg C m^{-2}	8.5 ± 0.2 (a)	6.5 ± 0.1 (b)	9.7 ± 0.1 (c)
	boreal	kg C m^{-2}	12.9 ± 0.5 (a)	7.7 ± 0.3 (b)	16.4 ± 0.5 (c)
	woody biome total	Pg C	797 ± 17 (a)	749 ± 11 (b)	975 ± 15 (c)

^aGPP, gross primary productivity; NPP, net primary productivity. Values are means for 2001–2006 (± 1 SE). Different letters denote statistical significant differences determined with a Tukey's HSD post hoc test at $\alpha = 0.05$.

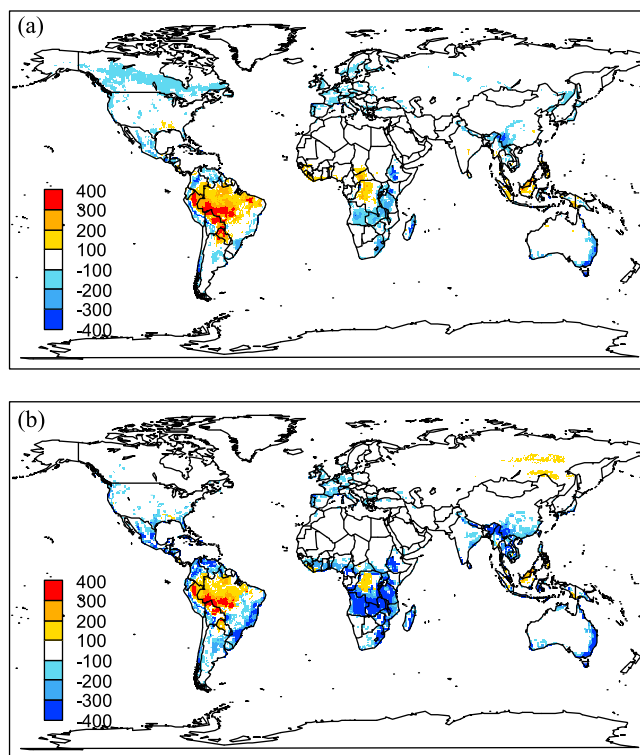


Figure 4. Difference in NPP ($\text{g C m}^{-2} \text{ yr}^{-1}$) estimated by Biome-BGC (MODIS) versus (a) the meta-analysis-based partitioning scheme and (b) VISIT (mean of 2001–2006). Note that the NPP estimate by Biome-BGC is used only as a reference, and this does not imply that Biome-BGC is more accurate than the other models.

partitioning scheme estimate of equilibrium woody biomass was 15% lower than the process-based models.

[19] We compared our equilibrium biomass (Table 3) estimates with *Luyssaert et al.* [2007] by calculating arithmetic means of their estimates of total forest biomass (above-ground and belowground) for tropical, temperate (humid, semiarid, and Mediterranean), and boreal (humid and semiarid) regions (14.3 ± 3.1 , 12.7 ± 2.1 , and $7.5 \pm 0.9 \text{ kg C m}^{-2}$, respectively). For tropical forests, their estimate is in the range of all three of the approaches used here. For temperate forests, results from three models obtained here are 24–49% lower than their estimate. For boreal forests, their estimate is within 3% of that from the meta-analysis-based partitioning scheme, but 42–54% lower than Biome-BGC and VISIT. These differences in equilibrium woody biomass, especially for temperate forests, may be due to the impacts of anthropogenic disturbances and land use. The observation sites in the work of *Luyssaert et al.* [2007] are almost exclusively from intact forests, but our input data (MODIS-based GPP) covers the entire terrestrial surface dominated by woody plants, including many areas where human impacts have significantly reduced forest productivity and standing biomass. While the data sets used by *Litton et al.* [2007] and *Luyssaert et al.* [2007] contain some overlap, the latter synthesis was based on a significantly larger data set ($n = 513$; compare to $n = 29$ in the work of *Litton et al.*) because it included

carbon budget estimates from eddy covariance techniques and simulation models in addition to field-based methods.

[20] Carbon use efficiency (NPP:GPP) values differed across models and biomes (Figure 7). While Biome BGC and VISIT relied on carbon use efficiency values that varied with temperature, carbon use efficiency of the meta-analysis-based partitioning scheme remained nearly constant throughout the entire biome gradient (0.43–0.45), where the small differences were the result of component specific partitioning of GPP to autotrophic respiration in foliage, stems, and roots. While carbon use efficiency was very similar across all models for tropical regions (0.41–0.45), Biome-BGC and VISIT estimated a higher carbon use efficiency than the meta-analysis-based partitioning scheme for colder biomes (0.54–0.56). Moreover, a large shift in carbon use efficiency for Biome-BGC occurred between tropical and temperate forests, while that for VISIT occurred between temperate and

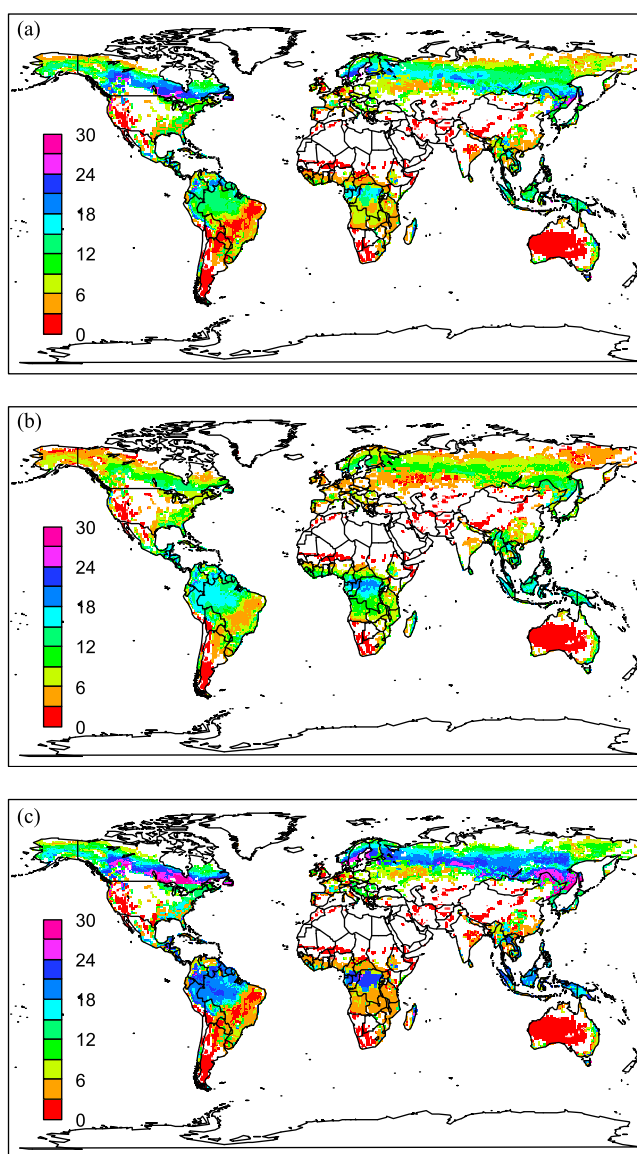


Figure 5. Total equilibrium biomass (kg C m^{-2}) from (a) Biome-BGC, (b) the meta-analysis-based partitioning scheme, and (c) VISIT (mean of 2001–2006).

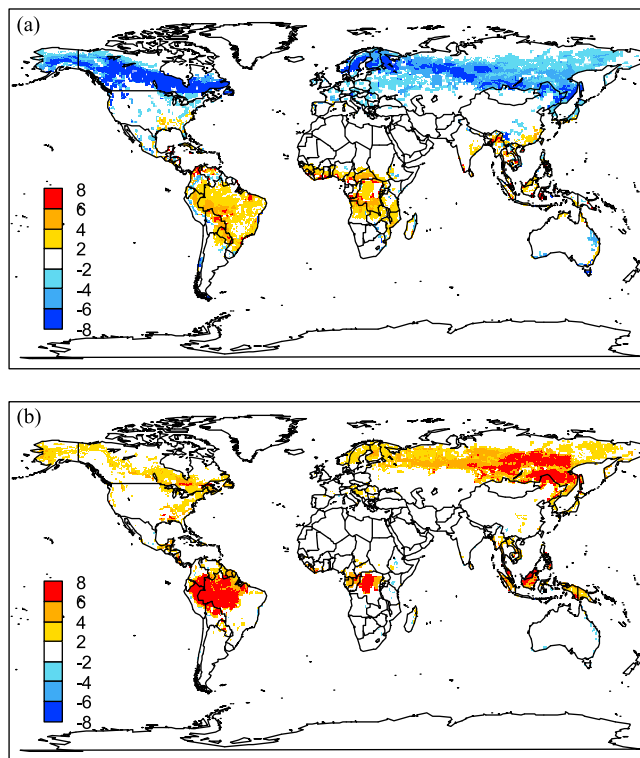


Figure 6. Difference in estimates of equilibrium biomass (kg C m^{-2}) from Biome-BGC (MODIS) versus (a) the meta-analysis-based partitioning scheme and (b) VISIT (mean of 2001–2006). Note that the NPP estimate by Biome-BGC is used only as a reference, and this does not imply that Biome-BGC is more accurate than the other models.

boreal forests. Of the three models, the pattern of carbon use efficiency for tropical, temperate, and boreal forests reported by *Malhi et al.* [1999] was closest to that of Biome-BGC. Differences between the meta-analysis based partitioning scheme and *Malhi et al.* [1999] are likely due to the number of stands examined: *Litton et al.* [2007] who utilized 29 available stand-level carbon budget studies, including the three stands (one stand from each biome) examined by *Malhi et al.* [1999].

[21] Sensitivity analyses of stem to root partitioning parameters in the meta-analysis-based partitioning scheme indicated that, due to differences in carbon use efficiencies of stem and root components, changes in c_i or c_s affected NPP estimates (Table 4). These differences in NPP were further propagated in equilibrium biomass due to the difference in tissue turnover time of stem versus roots (see Table 1). The response to the sensitivity analysis concerning c_i was monotonic, where higher c_i increased NPP and equilibrium biomass. This result directly reflected differences in stem and root parameters of carbon use efficiency and tissue turnover. In contrast, the sensitivity test on c_s demonstrated a heterogeneous response with respect to biome type. Since c_s controls stem to root partitioning as a function of productivity (GPP) in the meta-analysis-based partitioning scheme, tropical forests, a biome with overall high productivity, were the most impacted by choice of model. Changes in c_s caused a significant difference in equilibrium biomass estimates of

tropical forests while variation in temperate and boreal forests was minimal.

4. Discussion

[22] Comparing the three models, we found that the different algorithms employed for partitioning GPP to component tissues (foliage versus stems versus roots) and fluxes (respiration versus production) can significantly alter predictions of terrestrial carbon flux and stock in woody ecosystems, and thus the global carbon budget. In contrast to the process-based models, the meta-analysis-based model assumed no temperature dependence for respiration and displayed nearly constant carbon use efficiency for all forest types. Moreover, the process-based models calculate maintenance respiration rates as a function of living biomass while the meta-analysis-based partitioning scheme assumes no biomass dependency because *Litton et al.* [2007] did not identify a correlation between biomass and carbon partitioning across forest ecosystems. This difference in carbon use efficiency assumptions resulted in wide variations in global estimates of equilibrium woody biomass and NPP, as we had hypothesized. Because all models relied on the same MODIS GPP data set, variation across models resulted entirely from differences in model structure and starting assumptions. Notably, accurately modeling woody NPP and equilibrium biomass depends on correctly capturing both carbon partitioning patterns as well as estimating GPP. Here, we focused on the former because our aim was to highlight the model difference in carbon partitioning. However, future studies are needed to address the full suite of factors, including GPP, that control ecosystem carbon balance.

[23] Based on a literature review, *Prentice et al.* [2001] reported regional means and global totals of NPP and carbon stock in living biomass. The reported range of woody plant NPP from this prior study was $41.1\text{--}47.5 \text{ Pg C yr}^{-1}$, and outputs from all models in this analysis fall close to this range (Table 3). The range for woody plant carbon stock reported by *Prentice et al.* [2001] was $359\text{--}536 \text{ Pg C}$, with all three NPP estimation methods utilized here yielding higher estimates of woody plant biomass (Table 3). However, the plant carbon stock reported in this study is modeled to an equilibrium condition, even though a large fraction of terrestrial vegetation during the observation period (2001–2006) was below equilibrium values because of land use activities. Although GPP and NPP are also affected by anthropogenic activities, GPP and NPP generally have much shorter recovery times after disturbance compared to woody biomass [*Kashian et al.*, 2006]. Thus, the results from all methods employed here inherently overestimate the terrestrial plant carbon stock. As before, our objective was not to provide a new global estimate of equilibrium woody biomass, but rather to test how different carbon partitioning algorithms impact global estimates of woody biomass.

[24] The meta-analysis-based partitioning scheme assumes that ecosystem carbon use efficiency is constant across forest types, while Biome-BGC and VISIT vary carbon use efficiency as a function of biomass and temperature. A better understanding of environmental and physiological dependencies of carbon use efficiency is critical, as NPP:GPP has important ramifications for the flux and storage of carbon in terrestrial ecosystems. The meta-analysis-based partitioning

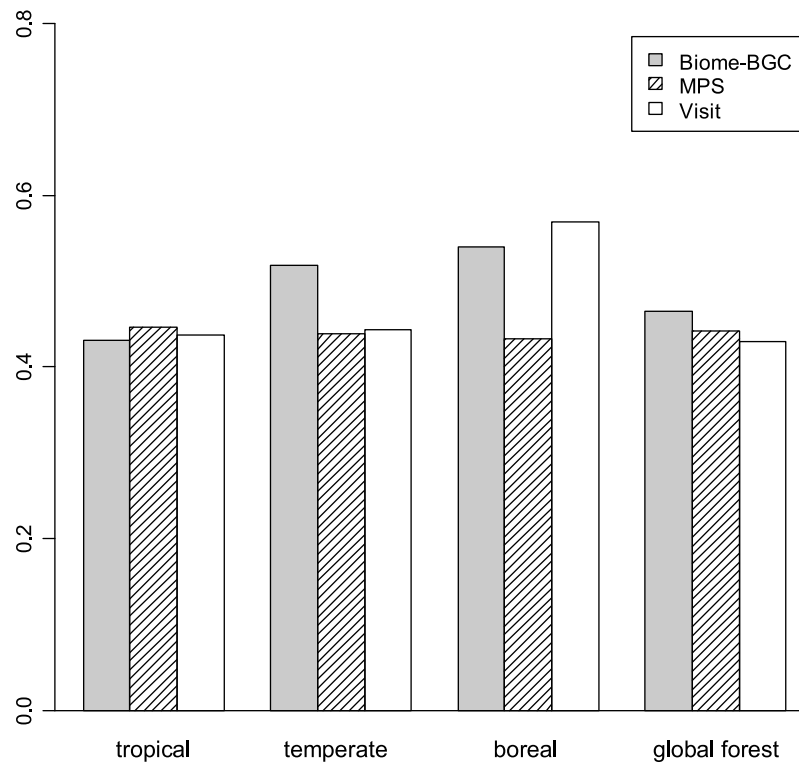


Figure 7. Carbon use efficiency (NPP/GPP) of woody plants by forest biome and for all forests globally. Values are means for 2001–2006.

scheme relies on a central tendency for carbon use efficiency of $0.43 (\pm 0.02 \text{ SE})$. This tendency is in line with findings of previous studies [Ryan *et al.*, 1996; Waring *et al.*, 1998; Amthor, 2000; Gifford, 2003; Curtis *et al.*, 2005] and suggests that carbon use efficiency does not vary with stand age, resource availability, aboveground biomass, or competition. In this analysis only central tendencies were considered in the parameterization as Monte Carlo type sensitivity analyses for all three outputs was beyond the scope of this study. While we relied on central tendencies, the carbon use efficiencies reviewed by Litton *et al.* [2007] ranged from 0.29 to 0.58 across diverse forest ecosystems, indicating that our current understanding of carbon use efficiency in forests is uncertain. In contrast to Litton *et al.* [2007], several studies, including two recent efforts, have documented that carbon use effi-

ciency can vary with forest type within a biome and with stand development [Ryan *et al.*, 1997; Makela and Valentine, 2001; DeLucia *et al.*, 2007; Zhang *et al.*, 2009].

[25] Whether NPP:GPP varies predictably with temperature, forest type, or stand age has important implications for modeling global carbon dynamics. DeLucia *et al.* [2007] used a database of carbon use efficiency calculated at 51 individual forest sites around the globe and found that carbon use efficiency was lowest in boreal forests (0.32), intermediate in tropical forests (0.46), and highest in temperate deciduous forests (0.59). In contrast, Zhang *et al.* [2009] used global estimates of GPP from MODIS and NPP derived from the temperature dependence of autotrophic respiration and found that the lowest values of carbon use efficiency were associated with broadleaf evergreen and

Table 4. Results of a Sensitivity Analysis on the Meta-Analysis-Based Partitioning Scheme for Carbon Partitioning of Stems Versus Roots^a

Variable	Region	Unit	Default	c_i		c_s	
				Minus	Plus	Minus	Plus
NPP	tropical	$\text{g C m}^{-2} \text{ yr}^{-1}$	950 ± 27	0.99 ± 0.01	1.02 ± 0.01	0.97 ± 0.01	1.03 ± 0.01
	temperate	$\text{g C m}^{-2} \text{ yr}^{-1}$	393 ± 5	0.98 ± 0.01	1.02 ± 0.01	0.99 ± 0.01	1.01 ± 0.01
	boreal	$\text{g C m}^{-2} \text{ yr}^{-1}$	238 ± 7	0.98 ± 0.03	1.02 ± 0.03	1.00 ± 0.03	1.00 ± 0.03
	woody biome total	Pg C yr^{-1}	48.1 ± 0.6	0.99 ± 0.01	1.02 ± 0.01	0.99 ± 0.01	1.02 ± 0.01
Equilibrium biomass	tropical	kg C m^{-2}	12.8 ± 0.2	0.90 ± 0.02	1.10 ± 0.02	0.81 ± 0.01	1.19 ± 0.02
	temperate	kg C m^{-2}	6.5 ± 0.1	0.86 ± 0.02	1.12 ± 0.02	0.95 ± 0.02	1.05 ± 0.02
	boreal	kg C m^{-2}	7.7 ± 0.3	0.87 ± 0.03	1.14 ± 0.04	1.04 ± 0.04	0.97 ± 0.04
	woody biome total	Pg C	749 ± 11	0.88 ± 0.01	1.12 ± 0.02	0.92 ± 0.01	1.09 ± 0.02

^aThe “intercept” parameter (c_i in equations (2) and (3)) was shifted by 20% above (plus) and below (minus) the default value of 0.194. The “slope” parameter (c_s) was doubled (plus) and zeroed (minus) from the default value of 5.06×10^{-5} . Here NPP and equilibrium biomass are reported as relative fractions (perturbed/default values).

deciduous forests growing in warm and wet sites (i.e., tropical forests; ~0.46–0.49) and that highest values were associated with needleleaf evergreen forests growing in cold and dry sites (i.e., boreal forests; ~0.58). In our study, the meta-analysis-based partitioning scheme estimates of carbon use efficiency varied minimally by forest type, as it was assumed to be constant by tissue component across all sites. For both the Biome-BGC and VISIT estimates, carbon use efficiency was highest in boreal forests (0.54–0.57) and lowest in tropical forests (0.43–0.44). In both of these models, as with Zhang *et al.* [2009], variability in carbon use efficiency across forest types was the result of the temperature dependence of autotrophic respiration. Clearly, this is an area that warrants further research, as global model estimates of forest carbon cycling often do not agree with the limited empirical data that is available from the few forest stands where carbon use efficiency has been estimated [e.g., Litton *et al.*, 2007; Ise and Sato, 2008].

[26] To quantify the effect of temperature dependence on autotrophic respiration, we experimentally simulated carbon use efficiency of tropical, temperate, and boreal forests in VISIT with temperature data from temperate forests. We selected grids that contained Manaus, Brazil (tropical), Duke Forest, United States (temperate), and Thompson, Manitoba, Canada (boreal). The default carbon use efficiency was 0.428, 0.436, and 0.568, respectively. We then used the temperature data from Duke Forest for all sites and obtained carbon use efficiencies of 0.496, 0.436, and 0.408. These results demonstrate that, without a temperature dependency of autotrophic respiration, carbon use efficiency tends to be higher in tropical forests and lower in boreal forests, as tropical trees allocate more carbon to structural components. However, as with the default carbon use efficiency, VISIT estimated lower carbon use efficiency for tropical forests due to the strong temperature dependency of autotrophic respiration.

[27] The relationships derived for the meta-analysis-based partitioning scheme were based primarily on empirical data, which demonstrated that carbon partitioning to stems and roots is dynamic in response to resource availability. This provides a potentially useful framework for designing a carbon partitioning scheme that is responsive to environmental change, as conventional algorithms often assume that aboveground versus belowground partitioning is constant. However, some components of the meta-analysis presented by Litton *et al.* [2007] were based on studies that made important assumptions about one or several components of carbon cycling. For example, most of the studies reviewed that estimated aboveground and belowground autotrophic respiration did so with gas exchange measurements and scaling techniques based on temperature and/or tissue nitrogen content, or similar gas exchange measurements and scaling techniques for maintenance respiration and growth respiration assuming a construction cost of 25% of net tissue production. In addition, major forest types of the various biomes, from tropical to boreal, were not equally represented in the meta-analysis on which the meta-analysis-based partitioning scheme was based. As a result, the simple statistical regressions used by the meta-analysis-based partitioning scheme may contain biases due to differences in data availability. We also highlight that the global patterns presented by Litton *et al.* [2007] may not be applicable for determining carbon partitioning coefficients for individual sites, as within-site

variability was large when resource availability was experimentally manipulated [e.g., Ryan *et al.*, 2004]. For individual sites reviewed by Litton *et al.* [2007] that manipulated resource availability, within-site changes in partitioning always agreed in direction but were typically much larger in magnitude than expected from the global, across-site relationship between GPP and partitioning employed here.

[28] In this study, we found that differences in how carbon partitioning is treated in terrestrial ecosystem models have an important influence on global woody NPP and equilibrium biomass estimates. Although our analysis was only for woody plants, this physiognomy type exerts a dominant influence on global terrestrial carbon cycling. More stand-level empirical studies on carbon partitioning are clearly needed to narrow uncertainties in carbon partitioning patterns and carbon use efficiency in woody plants, as are modeling studies that incorporate well studied carbon partitioning schemes. Importantly, the development and application of carbon partitioning schemes that consider environmental and plant taxonomic/functional variability are needed. In the interim, a simple and robust carbon partitioning scheme such as the meta-analysis-based partitioning scheme utilized here that is based on the best available data has the potential to greatly improve process-based models, with important implications for capacity to model and understand the role of terrestrial ecosystems in a rapidly changing world.

Appendix A

[29] VISIT estimates NPP from GPP, by subtracting maintenance respiration and growth respiration separately. First, the maintenance respiration has a temperature dependency (td):

$$td = \exp \left[\frac{T_{air} - 15}{10} \times \ln \left(2 \times e^{-0.009 \times (T_{air} - 15)} \right) \right] \quad (A1)$$

where T_{air} is monthly mean air temperature obtained from the Climate Research Unit database [New *et al.*, 2000]. The maintenance respiration is proportional to biomass of woody plant tissue (C_f , C_s , and C_r for foliage, stem, and biomass, respectively) with the temperature modifier td .

$$R_{mf} = k_{mf} \times td \times C_f \quad (A2)$$

$$R_{ms} = k_{ms} \times td \times C_s \quad (A3)$$

$$R_{mr} = k_{mr} \times td \times C_r \quad (A4)$$

While the respiration coefficient for foliage (k_{mf}) is constant (Table 1), that for stem (k_{ms}) and root (k_{mr}) are functions of the ratio of heartwood and sapwood.

$$k_{ms} = k_{mss} \times s_s + k_{msh} \times \frac{C_s - s_s}{C_s} \quad (A5)$$

$$k_{mr} = k_{mrs} \times s_r + k_{mrh} \times \frac{C_r - s_r}{C_r} \quad (A6)$$

where k_{mss} and k_{msh} are maintenance respiration fractions of stem sapwood and heartwood, respectively, and k_{mrs} and

k_{msr} are maintenance respiration fractions of root sapwood and heartwood, respectively. The mass of sapwood for stem (s_s) and root (s_r) are:

$$s_s = C_s \wedge \left[1 - \frac{C_s}{3 \cdot (50 + C_s)} \right] \quad (A7)$$

$$s_r = C_r \wedge \left[1 - \frac{C_r}{3 \cdot (50 + C_r)} \right] \quad (A8)$$

Thus, EPP , the amount of assimilated carbon available for growth processes (new biomass production and growth respiration) is calculated.

$$EPP = GPP - R_{mf} - R_{ms} - R_{mr} \quad (A9)$$

Then EPP is partitioned into EPP_f , EPP_s , and EPP_r , the growth partitioning to foliage, stem, and root, respectively.

$$EPP_f = EPP \times f_f \quad (A10)$$

$$EPP_s = (EPP - EPP_f) \times f_s \quad (A11)$$

$$EPP_r = EPP - EPP_f - EPP_s \quad (A12)$$

EPP_f is proportional to the growth allocation coefficient for foliage (f_f). The rest of EPP is partitioned into EPP_s and EPP_r by the growth allocation coefficient for stem (f_s). Finally, NPP of foliage, stem, and root (NPP_f , NPP_s , and NPP_r , respectively) are obtained by subtracting fractions of growth respiration for foliage, stem, and root (k_{gf} , k_{gs} , and k_{gr} , respectively).

$$NPP_f = (1 - k_{gf}) \times EPP_f \quad (A13)$$

$$NPP_s = (1 - k_{gs}) \times EPP_s \quad (A14)$$

$$NPP_r = (1 - k_{gr}) \times EPP_r \quad (A15)$$

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