

Plant Ecology & Diversity

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tped20>

Residence times of woody biomass in tropical forests

David Galbraith^{a b}, Yadvinder Malhi^b, Kofi Affum-Baffoe^f, Andrea D.A. Castanho^c, Christopher E. Doughty^b, Rosie A. Fisherⁱ, Simon L. Lewis^{a g}, Kelvin S.-H. Peh^{a e}, Oliver L. Phillips^a, Carlos A. Quesada^d, Bonaventure Sonké^h & Jon Lloyd^{a j}

^a School of Geography, University of Leeds, Leeds, UK

^b Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK

^c Woods Hole Research Center, Falmouth, Massachusetts, USA

^d Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil

^e Department of Zoology, University of Cambridge, Cambridge, UK

^f Forestry Commission, Ghana, Resource Management Support Centre, Kumasi Ghana

^g University College London, London, UK

^h Plant Systematic and Ecology Laboratory, Higher Teacher's Training College, University of Yaoundé I, Yaoundé Cameroon

ⁱ National Center for Atmospheric Research, Boulder, Colorado, USA

^j Centre for Tropical Environmental and Sustainability Science (TESS) and School of Earth and Environmental Sciences, James Cook University, Cairns, Australia

Accepted author version posted online: 28 Jan 2013. Version of record first published: 25 Mar 2013.

To cite this article: David Galbraith, Yadvinder Malhi, Kofi Affum-Baffoe, Andrea D.A. Castanho, Christopher E. Doughty, Rosie A. Fisher, Simon L. Lewis, Kelvin S.-H. Peh, Oliver L. Phillips, Carlos A. Quesada, Bonaventure Sonké & Jon Lloyd (2013): Residence times of woody biomass in tropical forests, *Plant Ecology & Diversity*, DOI:10.1080/17550874.2013.770578

To link to this article: <http://dx.doi.org/10.1080/17550874.2013.770578>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Residence times of woody biomass in tropical forests

David Galbraith^{a,b,*}, Yadvinder Malhi^b, Kofi Affum-Baffoe^f, Andrea D.A. Castanho^c, Christopher E. Doughty^b, Rosie A. Fisherⁱ, Simon L. Lewis^{a,g}, Kelvin S.-H. Peh^{a,c}, Oliver L. Phillips^a, Carlos A. Quesada^d, Bonaventure Sonké^h and Jon Lloyd^{a,j}

^aSchool of Geography, University of Leeds, Leeds, UK; ^bEnvironmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK; ^cWoods Hole Research Center, Falmouth, Massachusetts, USA; ^dInstituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil; ^eDepartment of Zoology, University of Cambridge, Cambridge, UK; ^fForestry Commission, Ghana, Resource Management Support Centre, Kumasi Ghana; ^gUniversity College London, London, UK; ^hPlant Systematic and Ecology Laboratory, Higher Teacher's Training College, University of Yaoundé I, Yaoundé Cameroon; ⁱNational Center for Atmospheric Research, Boulder, Colorado, USA; ^jCentre for Tropical Environmental and Sustainability Science (TESS) and School of Earth and Environmental Sciences, James Cook University, Cairns, Australia

(Received 7 September 2012; final version received 23 January 2013)

Background: The woody biomass residence time (τ_w) of an ecosystem is an important variable for accurately simulating its biomass stocks.

Methods and results: We reviewed published data from 177 forest plots across the tropics and found a six-fold variation (23–129 years) in τ_w across our dataset, with a median τ_w of ca. 50 years. This value is similar to the median default value across 21 vegetation models for tropical forests, although the range of values used in models is large (20 to 200 years).

Conclusions: The notion of a constant τ_w across all tropical forests may be of limited utility, given the large observed variation in τ_w . We found that while there was little relationship between climate variables and τ_w , there was evidence that edaphic factors exerted a strong influence on τ_w . In both the Neotropics and the Paleotropics, τ_w was highest in heavily weathered soils, suggesting that low soil fertility and/or non-limiting soil physical conditions exert a critical influence on τ_w . There is considerable uncertainty in how τ_w will be affected by global environmental change, especially by increased atmospheric CO₂. Even small changes in τ_w could significantly reduce the future tropical forest carbon sink predicted by many vegetation models.

Keywords: biomass; dynamic vegetation models - DVGMS; ecosystem models; residence time; tropical forest

Introduction

Tropical forests play a pivotal role in the global carbon cycle. They are responsible for approximately one-third of global terrestrial gross primary productivity (Beer et al. 2010) and a similar proportion of global net primary productivity (Roy and Saugier 2001). Moreover, they potentially exert a strong influence over global patterns of inter-annual variability in net primary productivity (Zhao and Running 2010). Tropical forests store an estimated 250 Pg of carbon (C) in their biomass, equivalent to 40–50% of the total amount of C stored in terrestrial vegetation (Prentice 2001; Pan et al. 2011; Saatchi et al. 2011). Field measurements from a network of census plots across Amazonia (Baker et al. 2004, Phillips et al. 2008) and Africa (Lewis et al. 2009a) suggest that old-growth tropical forests are gaining in biomass, at a rate of ca. 0.5 Mg C ha⁻¹ year⁻¹. Across tropical forests, this represents a carbon sink of a similar magnitude to the total emissions due to deforestation (Malhi 2010). Understanding the nature and future behaviour of this carbon sink has become an important issue in tropical ecosystem ecology. Although uncertainties remain, most ecologists now agree that at least some of this tropical forest carbon sink exists as a consequence

of an on-going stimulation of their net primary productivity (N_P), probably in response to increasing atmospheric CO₂.

Any 'additional' carbon assimilated through this CO₂ fertilisation effect must, of course, eventually return to the atmosphere because trees within a forest stand are continually dying and decomposing. Thus, it is not only the magnitude of any growth stimulation, but also the average amount of time a carbon atom spends as living structural dry matter within an ecosystem (before returning to the atmosphere), the mean residence time (τ), that determines the magnitude of any carbon sink (Lloyd and Farquhar 1996; Lloyd 1999). Thus, although many climate/vegetation model simulations suggest that this tropical sink will persist until the end of the twenty-first century (e.g. Gumpenberger et al. 2010; Rammig et al. 2010), this will only occur if increases in forest growth rates are not offset by a reduction in τ .

Standing biomass stocks represent a balance between a number of processes that lead to biomass accumulation or to biomass loss (Malhi et al. 2011; Figure 1). These include the total net primary productivity (N_P), itself a function of gross primary productivity (G_P) and the carbon use efficiency (N_P/G_P), as well as the allocation of N_P into different plant organs and the mean residence time of

*Corresponding author. Email: d.r.galbraith@leeds.ac.uk

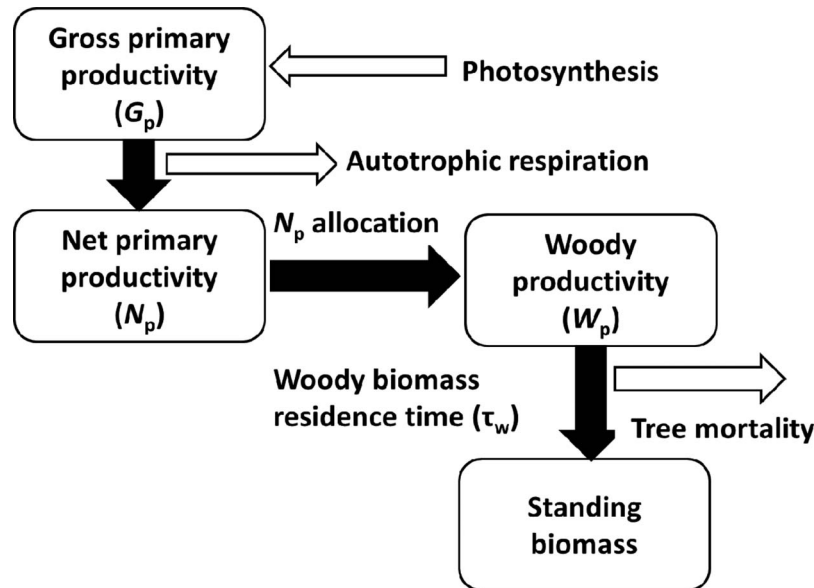


Figure 1. Schematic diagram of the chain of processes that contribute towards vegetation biomass storage. Reproduced from Malhi et al. (2011).

carbon stored in different plant organs (Lloyd and Farquhar 1996). Recently, Malhi et al. (2011) conducted a review of published data from tropical forests on the allocation of N_p into different plant tissues (canopy, wood and fine roots) and compared the data with allocation patterns from vegetation models. In this paper, we focus on the mean residence time of woody biomass (τ_w); this being the average period of time that carbon is locked up in the living woody biomass of an ecosystem before it is transferred to the litter or necromass pool. As the greatest part of forest biomass is stored in woody tissue, the allocation of N_p to woody biomass and τ_w are particularly important variables to represent correctly in vegetation models for accurate simulation of ecosystem biomass stocks. Our overall aim in this paper was to review the published literature on τ_w for both Neotropical and Paleotropical forests in a way that will inform the representation of this important component of the carbon cycle in global vegetation models. We focus on mean τ_w in this paper, as most of the published data are presented at forest plot level, but recognise that τ_w can vary significantly within individual forest plots due to compositional differences (e.g. Hart 2012).

In this review, we address the following specific questions:

- (1) What is a 'typical' τ_w for tropical forests?
- (2) What drives the spatial variation in τ_w across tropical forest plots?
- (3) How is τ_w related to other ecosystem variables such as woody productivity (W_p) and N_p allocation to wood, (new growth of boles and branches)?
- (4) How well do vegetation models represent observed τ_w values for tropical forests?
- (5) How might tropical forest τ_w be affected by global environmental change?

The first question is of interest because many global vegetation models (e.g. many of the models in Table 1) assume that forest trees can be described as one or two plant functional types (PFTs), and that the woody biomass residence time of these PFTs is an invariant parameter in space and in time. For such models, it is important that parameter values assumed are representative of the woody biomass residence time of an 'average' tropical forest.

The second question is of interest as there is growing awareness of the limitations associated with assuming fixed τ_w in vegetation models, as these can lead to inaccurate simulation of spatial gradients in forest biomass (e.g. Delbart et al. 2010). In some cases, models may simulate above-ground biomass stocks reasonably well, through compensation of errors in underlying processes. This was recently shown by Delbart et al. (2010) with the ORCHIDEE model, who found that the model over-estimated average above-ground woody N_p in Amazonia by > 60% but simulated acceptable above-ground biomass through assuming a mean residence time in the model that was much too low relative to observations. If one is to have confidence in future predictions of forest biomass storage by vegetation models, then the models must be able to simulate biomass dynamics for the correct reasons (i.e. they must be able to simulate allocation processes and mortality processes correctly). Ultimately, this entails understanding what drives the spatial and temporal variation in both of these processes. In this paper, we focus on two potential drivers of spatial variation in τ_w for tropical forests: climate and soils.

The third question is important as it may provide new insights into tropical forest functioning, and may lead to improved modelling of the relationships between different ecosystem variables. The fourth question directly relates to the ability of vegetation models to simulate observed

Table 1. Representation of woody biomass residence times (τ) of dominant plant functional types (PFTs) over tropical forests in 27 global vegetation models..

Model name	Dominant tropical forest PFT	General approach	Key equation(s)	Reference
aDGVm	Tropical forest	Background woody biomass residence time (τ_w^*) with additional mortality due to negative carbon balance, competition and fire	$\tau_w^* = 25$ years	Scheiter and Higgins (2009)
BIOME-BGC	Tropical evergreen broadleaf forest	Fixed annual mortality rate (λ)	$\lambda = 0.03 \text{ year}^{-1}$ ($\tau_w = 33.3$ years)	Ichii et al. 2007
CARAIB	Tropical broadleaf forest	Fixed woody biomass residence time (τ_w)	$\tau_w = 150$ years	Warnant et al. 1994
CARLUC	(Amazon) tropical forest	Fixed woody biomass residence time (τ_w)	$\tau_w = 50$ years	Hirsch et al. 2004
CASA	Evergreen broadleaf forest	Fixed woody biomass residence time (τ_w)	$\tau_w = 60$ years	Wang et al. 2010
CLM-DGVM	Tropical broadleaf evergreen forest	Same as LPJ	Same as LPJ	Levis et al. 2004
CNCLASS	Tropical broadleaf forest	Fixed woody biomass residence time (τ_w)	$\tau_w = 20$ years	Arain et al. 2006
CTEM	Broadleaf evergreen forest	Four modes of mortality: age related (λ_a), low growth efficiency (λ_g), unfavourable climate (λ_c), exogenous disturbance (λ_d)	$\lambda = \lambda_a + \lambda_g + \lambda_c + \lambda_d$	Arora and Boer 2006
ED	Tropical forest with three successional types: pioneer, mid-successional and late-successional	Background mortality (λ_i) for different successional types with additional mortality due to negative carbon balance	$\lambda_i = 0.014 + 0.15(1 - \rho_i/0.9)(\rho_i$ is the wood density of the successional type; τ ranges from 15 years for pioneers to 75 years for late successional types)	Moorcroft et al. 2001
Frankfurt Biosphere Model	Tropical evergreen forest	Fixed woody biomass residence time (τ_w)	$\tau_w = 41.1$ years	Kohlmaier et al. 1997
GTEC	Tropical evergreen forest	Fixed woody biomass residence time (τ_w)	$\tau_w = 50$ years	Post et al. 1997
HRBM	Tropical forest	Fixed woody biomass residence time (τ_w)	$\tau_w = 200$ years	Kaduk and Heimann 1996
Hyland	Broadleaf forest	Fixed woody biomass residence time (τ_w)	$\tau_w = 20$ years	Levy et al. 2004; Peter Levy pers. comm.
Hybrid v. 3.0/4.1	Broadleaved evergreen tree	Fixed background woody biomass residence (τ_w^*) and background tree mortality rate (λ); additional mortality due to negative carbon balance, drought and embolism	$\tau_w^* = 100$ years; $\lambda = 0.0025\% \text{ year}^{-1}$	Friend et al. 1997; Friend and White 2000
IBIS (current)	Tropical broadleaf evergreen forest	Fixed woody biomass residence time (τ_w)	$\tau_w = 25$ years	Hewley Imbuzeiro, pers. comm.
IBIS (original)	Tropical broadleaf evergreen forest	Fixed woody biomass residence time (τ_w)	$\tau_w = 50$ years	Foley et al. 1996
JS-BACH	Tropical evergreen broadleaf forest	Fixed woody biomass residence time (τ_w)	$\tau_w = 100$ years	Cited in Wolfe et al. 2011
JULES-TRIFFID	Broadleaf forest	Fixed background woody biomass residence time (τ_w^*) and fixed background disturbance rate (λ)	$\tau_w^* = 200$ years $\lambda = 0.005\% \text{ year}^{-1}$	Clark et al. 2011
LM3V	Tropical forest	Background woody biomass residence time (τ_w^*) with additional mortality due to fire	$\tau_w^* = 40$ years	Shevliakova et al. (2009)
LPJ	Tropical broadleaf evergreen forest	Mortality due to negative carbon balance (λ_{NPP}), low growth efficiency (λ_g), light competition (λ_l), heat stress (λ_h), unfavourable climate (λ_c) and fire (λ_{fire})	$\lambda = \lambda_{NPP} + \lambda_g + \lambda_l + \lambda_h + \lambda_c + \lambda_{fire}$	Sitch et al. 2003

(Continued)

Table 1. (Continued)

Model name	Dominant tropical forest PFT	General approach	Key equation(s)	Reference
LPJ-GUESS	Tropical broadleaf evergreen forest	Mortality due to stress(λ_{stress}), light competition (λ_l) and fire disturbance as well as background mortality($\lambda_{\text{background}}$)	$\lambda = \lambda_{\text{background}} + \lambda_{\text{stress}} + \lambda_l + \lambda_{\text{fire}}$	Smith et al. 2001
MOSES-TRIFFID	Broadleaf forest	Fixed woody biomass residence time (τ_w^*) and fixed background disturbance rate (λ)	$\tau_w^* = 100 \text{ years}$ $\lambda = 0.004\% \text{ year}^{-1}$	Cox 2001
ORCHIDEE (current)	Tropical broadleaf evergreen forest	Fixed woody biomass residence time (τ_w)	$\tau = 30 \text{ years}$	Nicolas Delbart, pers. comm.
ORCHIDEE (original)	Tropical broadleaf evergreen forest	Same as LPJ	Same as LPJ	Krinner et al. 2005
SEIB-DGVM	Tropical broadleaf evergreen forest	Mortality due to aging (λ_a), growth inefficiency (λ_g) and gap dynamics (λ_{gap})	Maximum tree lifespan ranges from 50 years in pioneers to 200 years in late-successional trees; $\lambda_g = \max(0.0178^* \exp(-242.57 \times \Delta \text{dbh}), 0.0032)^* \alpha$ (Δdbh is the annual diameter increment and α is a multiplier that accounts for differential mortality rates across PFTs)	Sato 2009
SIB-CASA	Tropical forest	Fixed woody biomass residence time (τ_w)	$\tau_w = 58 \text{ years}$	Schaefer et al. 2008
VISIT	Tropical forest	Fixed woody biomass residence time (τ_w)	$\tau_w = 29.24 \text{ years}$	Ise et al. 2010

biomass dynamics. The fifth question is of interest for modelling the future dynamics of tropical forests. We discuss both the potential effects of elevated atmospheric CO₂ and climate change associated with increased concentrations of atmospheric greenhouse gases on tropical forest τ_w .

Methods

The concept of woody biomass residence time

Model descriptions of woody biomass residence time. Most vegetation models (e.g. Foley et al. 1996; Cox 2001; Sitch et al. 2003; Levy et al. 2004) simulate at least three vegetation biomass pools: wood, leaves and fine roots. In its simplest form, the change in the biomass (M) of an individual plant compartment i over a period of time can be described as:

$$\frac{dM_i}{dt} = \alpha_i N_P - \frac{M_i}{\tau_i}, \quad (1)$$

where α_i represents the fraction of net primary productivity (N_P) allocated to the biomass pool i , and τ_i is the mean residence time of that biomass pool, usually expressed in years (Kohlmaier et al. 1987; Lloyd and Farquhar 1996). Several global vegetation models assume that the residence times of these pools are fixed for a given PFT (e.g. Foley et al. 1996; Cox 2001; Levy et al. 2004; Delbart et al. 2010). The annual biomass turnover rate ($1/\tau$) in these models represents the average proportion of biomass lost through abscission or herbivory in the case of foliage or fine roots, while the woody biomass turnover rate ($1/\tau_w$) is a proxy for losses of biomass due to whole-tree mortality, implicitly also including abscission of branches. In the steady state ($dM_i/dt = 0$) rates of new production are exactly balanced by rates of loss. As the vast majority of the biomass of a forest is stored in long-lived woody tissue, the choice of parameter value chosen for the residence time of woody biomass, τ_w , is critically important for simulating biomass stocks correctly. Usually, global vegetation models do not simulate forest structure in any great detail, but rather simulate vegetated 'areas' with average characteristics, such as carbon content and leaf area index. Woody biomass in these models is treated as one large aggregated pool, leading Wolf et al. (2011) to refer to them as 'big wood models'. These models are often run over large geographical areas and thus need to capture 'average' vegetation properties across those areas.

In recent years, a number of vegetation models have been developed as alternatives to 'big wood models' in that they simulate individual trees or cohorts of trees as opposed to aggregated carbon pools (Moorcroft et al. 2001; Smith et al. 2001; Sitch et al. 2003; Sato et al. 2007). These models are often associated with more sophisticated descriptions of tree mortality (McDowell et al. 2011), which has been represented as a function of growth efficiency (e.g. Sitch et al. 2003; Sato 2009), climatic thresholds (e.g. Sitch et al. 2003; Arora and Boer 2006) and more recently through a carbon starvation mechanism (Fisher

et al. 2010). In each case, the models calculate a background tree mortality rate which increases under climatic stress.

Estimating woody biomass residence time from the field data. Many of the parameterisations commonly used in global vegetation models have remained relatively static since they were created in the 1990s or in the early 2000s, this being a time when few relevant field data existed for tropical forests. In the last decade, however, a very large amount of information on tropical forest dynamics has become available, particularly through the creation of networks of permanent sampling plots in Amazonia (Malhi et al. 2002) and other tropical forest regions (Chave et al. 2008; Lewis et al. 2009a). Thus reasonable values of τ_w for tropical forests can now be estimated with a much greater degree of accuracy than was previously possible. We here aggregate the data available to date, providing updated data-constrained parameter estimates with a view to improving the fidelity of parameterisations in existing dynamic vegetation models.

Based on 'reservoir theory' (Nir and Lewis 1975), the most common approach for estimating τ_w is to calculate the woody biomass residence time as the ratio of mean standing woody biomass (\bar{M}_w) and mean woody productivity (\bar{W}_p):

$$\tau_w = \frac{\bar{M}_w}{\bar{W}_p}. \quad (2)$$

The \bar{W}_p term above is the sum of the stem growth of standing vegetation and a small recruitment term (Malhi et al. 2004). This approach for calculating τ_w is valid only for near-equilibrium systems, such as old-growth tropical forests and will not work, for example, in systems such as secondary forests where standing biomass stocks are below equilibrium values (Lloyd 1999; Malhi 2012).

Field estimates of forest biomass are usually generated through allometric equations which estimate biomass through relationships with easily measurable tree properties, such as tree height and/or diameter at breast height (Chambers et al. 2004; Feldpausch et al. 2011) and in some cases wood density (Baker et al. 2004). These allometric equations are usually applicable to above-ground biomass only, and relatively crude approaches based on multiplying factors are used to calculate below-ground woody biomass and productivity (e.g. Malhi et al. 2009a; Metcalfe et al. 2010). An alternative approach to estimate τ_w , which bypasses the need for specific allometric equations, is to simply divide the plot basal area by basal area productivity (Malhi et al. 2004).

Relating woody biomass residence time to tree mortality rates. A metric related to τ_w is the mean stem residence time τ_s , a measure of the mean lifetime of individual trees, defined as:

$$\tau_s \sim \frac{1}{\lambda}, \quad (3)$$

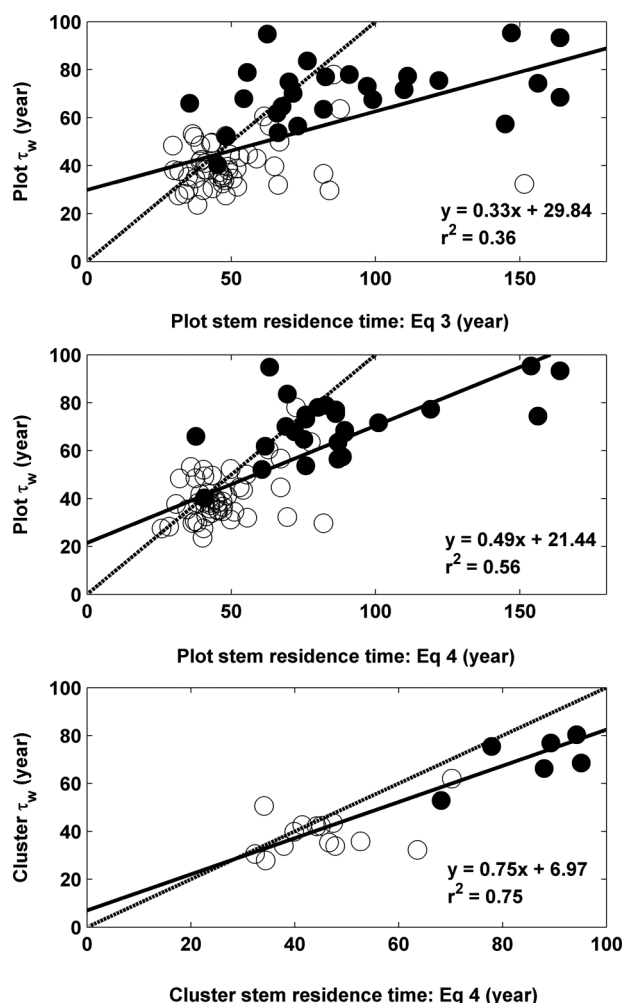


Figure 2. The relationship between stem residence time (τ_s) and woody biomass residence time (τ_w) for (top panel) 74 Amazonian plots and with stem residence time equivalent to 1/annual stem mortality (Equation (3)) ($P < 0.001$), (middle panel) 74 Amazonian plots with stem residence time equivalent to 1/annual stem turnover (Equation (4)) ($P < 0.001$) and (bottom panel) 20 clusters of two or more plots with stem residence time equivalent to 1/annual stem turnover (Equation (4)) ($P < 0.001$). Solid lines represent the lines of best fit through the data and dashed lines represent the 1:1 lines. Each point in the bottom panel represents the biomass-weighted harmonic mean of two or more plots. Open circles denote points from western Amazonia (located west of Manaus) while closed circles are points in central/eastern Amazonia (plots located around and east of Manaus).

where $\bar{\lambda}$ is the background mean annual mortality rate, defined as the average proportion of trees within the population dying each year and as calculated according to Sheil and May (1996). The relationship between τ_s as calculated by Equation (3), and τ_w as calculated by Equation (2) is shown in Figure 2(a) for 74 old-growth forest plots in Amazonia for which mortality, biomass and woody productivity data were available (Malhi et al. 2004; Phillips et al. 2004; Keeling and Phillips 2007). It is obvious that the relationship deviates considerably from a 1:1 relationship, and that there is also considerable scatter in the relationship. One reason for this may be the stochastic nature of mortality events, which means that inter-annual fluctuations in

tree mortality tend to be greater than fluctuations in productivity; thus, more census intervals are required to determine a baseline $\bar{\lambda}$ than is the case for W_P (and hence τ_w). Several studies reported stem turnover rates, calculated as the average of mortality and recruitment rates, besides mortality rates (e.g. Phillips 1996; Lewis et al. 2004a; Phillips et al. 2004). In theory, mortality and recruitment rates should be equivalent for forests in equilibrium conditions, although this may not be evident over a small number of census intervals or when monitoring plots of small size. Stem turnover values should therefore provide more representative values of background stem mortality rates than just the measured stem mortality rates over a few census intervals. Stem residence time can therefore also be calculated, presumably more accurately, as:

$$\tau_s = \frac{1}{(\bar{\mu} + \bar{\lambda})/2} \quad (4)$$

where $\bar{\mu}$ is the mean background stem recruitment rate and mean stem turnover rate is $(\bar{\lambda} + \bar{\mu})/2$.

The relationship between woody biomass residence time and stem residence time is much stronger if stem residence time is calculated as in Equation (4) ($r^2 = 0.56$) instead of Equation (3) ($r^2 = 0.36$) but still with substantial scatter (Figure 2(b)). A more robust measure of background mortality can be obtained if one considers clusters of plots rather than individual plots as the measurement unit, thus sampling a larger area in each cluster and thus dampening stochastic mortality effects. Most (62/74) of the plots used to construct Figure 2 occurred in 20 clusters of two or more plots, and after pooling such nearby plots together, simple least squares regression indicated a strong, significant relationship between cluster-based estimates of calculated by Equation (4) and cluster-based estimates of woody productivity as calculated by Equation (2) ($r^2 = 0.75$, $P < 0.001$). The seasonally flooded Las Londras (LSL) cluster was a clear outlier in this relationship as τ_s was considerably (95%) greater than τ_w . The relationship between τ_s and τ_w as calculated for these clusters of plots is shown in Figure 2(c). This relationship was significantly different from a 1:1 relationship, and τ_s was found to be on average 14% greater than τ_w , once the outlier cluster (LSL) was removed from the analysis. Assuming negligible measurement errors, this result implies that, on average, the probability of death is greater for larger trees within a stand, with this effect being particularly marked for stands with a high τ_w . However, differences in the relationship between τ_s and τ_w exist between western Amazonian clusters and central/eastern Amazonian clusters, with the former being much closer to a 1:1 relationship than the latter (Figure 2). A 1:1 relationship implies equal probability of death across all size classes, whereas $\tau_s > \tau_w$ suggests that the probability of death of larger trees is greater than that of smaller trees. Our results are generally supported by data from Vieira et al. (2005), who found that the mean age of individual trees in three Amazonian sites was greater than the mean woody biomass residence times, and Chao

et al. (2008), who found that the probability of tree mortality increased with size in north-eastern Amazonian forests but not in north-western Amazonian forests, where there was no obvious size effect influencing observed mortality patterns. Results from other studies outside of Amazonia, however, have been much less clear, with some sites showing increasing mortality with size while others showed decreasing mortality with size (e.g. Muller-Landau et al. 2006).

Compilation of published data on woody biomass residence time and analysis

We compiled a dataset of woody biomass residence time (τ_w) for old-growth tropical forests across the tropics. We excluded sites that had suffered catastrophic damage due to natural disturbances, such as hurricanes. Some of the sites in the dataset have been affected by recent droughts, but for these sites we used only data from periods before the drought event, if pre-drought and drought data were reported separately. We note that some of the Australian sites in our database have been logged in the past (Vancley 1991) and for these plots we only used the data reported in Lewis et al. (2004a), which are based on census intervals where no logging took place. We prioritised sites where data on standing biomass and W_P were both measured but also included sites in our database for which only information on stem turnover was available. We did not include any plots in our database where woody productivity was inferred from other productivity measures, such as litterfall. This was common practice in a number of early studies (e.g. several of those reported in Clark et al. 2001). Given the small-scale patchiness of above-ground biomass that can occur in tropical forests (e.g. Chave et al. 2001), we only considered plots that were ≥ 0.2 ha in area, as was done in Lewis et al. (2009a).

We drew upon several studies that published data for multiple sites (Clark et al. 2001; Lewis et al. 2004a; Malhi et al. 2004; Keeling and Phillips 2007; Chave et al. 2008) and also a few additional studies for single plots or clusters of plots. As shown in the preceding section, there is considerable scatter in the plot-based relationship between stem residence time and woody biomass residence time (Figure 2(a), (b)), but the relationship is much more robust when cluster means are used instead of plot values (Figure 2(c)). We therefore only used the stem mortality

data if these were reported for plots occurring in clusters of two or more plots or if a single plot reported measurements from ≥ 3 census intervals. Clusters of plots where only τ_s were available were given the same weighting in our analysis as single plots for which woody biomass residence time could be calculated directly from biomass and productivity data. We used the empirical relationship in Figure 2(c) to convert τ_s , calculated as the reciprocal of stem turnover when turnover was available and the reciprocal of stem mortality when turnover was not provided, to τ_w . Following this procedure, our database consisted of a total of 177 plots (including clusters of plots where only stem turnover was reported). Of these, 124 (70.0%) were located in the Americas, 29 (16.4%) were located in Asia, 21 (11.9%) were located in Africa and three were located in Australia (1.7%). Data and further descriptions of the plots in our database are provided in Tables S1 and S2; a map of plot locations is shown in Figure 3.

To ensure consistency across our dataset, it was necessary to apply additional corrections to the productivity data for some of the sites. W_P is the sum of recruitment and stem wood increment. Although τ_w was reported directly for many sites (e.g. those obtained from the dataset compiled by Malhi et al. (2004)), some sites only presented information on above-ground stem biomass increment without considering recruitment. For these sites, we applied a simple multiplier correction (total woody productivity (≥ 10 cm dbh) = stem biomass growth (≥ 10 cm dbh) * 1.12), derived from the Chave et al. (2008) dataset, for which both recruitment and stem production data were available. Plots for which woody biomass residence time was calculated indirectly from stem turnover rates were not corrected for this effect, as the equation used to convert from stem residence to woody biomass residence times (Figure 2(c)) was derived exclusively from points for which the recruitment term was included in the woody productivity values. A second correction was necessary to account for the influence of census interval length on W_P estimation. This was done following the four-step procedure outlined in Malhi et al. (2004) but applied to woody productivity rather than basal area growth rate as was done in the original paper. A similar procedure was carried out by Phillips et al. (2009) and Aragão et al. (2009). Stem turnover rates are also influenced by census interval lengths, and where necessary these were corrected using the census interval length correction developed by Lewis et al. (2004a) before being converted

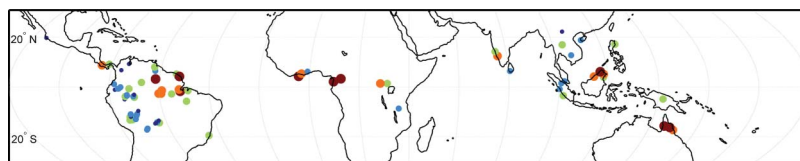


Figure 3. Geographical locations of the clusters of plots in our dataset, fully described in Table S1 (available as online supplementary material). Points are of different colours and sizes to reflect differences in woody biomass residence time (τ_w). Dark blue, τ_w of 20–35 years; light blue, τ_w of 35–50 years; green, τ_w of 50–65 years; orange, τ_w of 65–80 years; brown, $\tau_w > 80$ years. For clarity, the size of the dots is increased as residence time becomes progressively greater so that brown dots are the largest and dark blue dots are the smallest. The coordinates of some points have been adjusted slightly to enhance visibility.

to woody biomass residence time. The implications of this census interval effect are discussed in detail in several previous studies (Lewis et al. 2004a; Malhi et al. 2004; Phillips et al. 2009) and we do not address this issue further in this paper.

One aim of this paper was to compare the representation of ‘default’ woody biomass residence times in vegetation models with published data from our literature review. We thus collated information on descriptions of woody biomass residence time of tropical forests in 27 vegetation models that have been used to make global or regional assessments of the carbon cycle. In most cases, these models adopt a fixed τ_w but some models do have explicit mortality terms which allow for changing τ_w values (Table 1). For models that assume a fixed τ_w for all tropical forests, it is important that the parameters values provided for τ_w represent ‘typical’ tropical forests. This is complicated because sampling plots are not uniformly distributed across tropical forests (Figure 3). As many of the plots in our dataset are highly clustered in space, the mean (or median) value of woody biomass residence time across plots may be biased by clusters of plots which contain a large number of plots. To minimise this effect, we grouped plots into clusters (Table S1) and analysed the woody biomass residence time on a cluster basis ($n = 83$) as well as a plot basis ($n = 177$). Clusters represent groups of plots where typically the maximum inter-plot distance is not greater than 5 km (Phillips et al. 2009). We consider cluster values to be less vulnerable to geographic bias and more likely to provide more robust estimates of ‘average’ woody biomass residence times in the tropics. Each cluster consisted of between 1 and 11 plots. When calculating cluster means, we always took the biomass-weighted harmonic mean, this being the mathematically correct means for the estimation of an aggregated τ (Lloyd 1999).

To explore the underlying drivers of spatial variation in woody biomass residence times, we examined relationships between τ_w and elevation and climate (annual rainfall, mean annual temperature) as well as relationships with soil type. Soil type and climate information were also gathered for each site from the original publications,

although this information was not available for all sites. Climate data (rainfall and temperature) were obtained from the Climate Research Unit TS 3.0 gridded global dataset (Mitchell and Jones 2005) when not reported in the original papers. We also investigated the relationship between τ_w and W_p and the fraction of total N_p allocated to stem growth. To examine the drivers in geographical variation of woody biomass residence time, we clustered together nearby plots located on similar soil types so as to minimise spatial autocorrelation.

We used linear regression analyses to assess the relationships between τ_w , τ_s , N_p allocation to stem growth and W_p . Non-parametric correlation analyses (Kendall’s rank correlation coefficient, $-T$, and Spearman’s rank correlation coefficient, ρ) were used to assess associations between τ_w and climate variables (mean annual rainfall and temperature). Kruskal–Wallis non-parametric ANOVA was used to assess differences in τ_w among continents and among different soil fertility categories. We computed 0.95 confidence intervals for summary statistics (arithmetic mean, harmonic mean and median) based on 10,000 bootstrap samples.

Results and discussion

What is the ‘typical’ woody biomass residence time of tropical forests?

The arithmetic mean τ_w across all plots ($n = 177$) in our database was 60 years (bootstrapped 0.95 confidence intervals: [56, 64]) while the harmonic mean and median values were 51 [48, 54] and 55 [49, 60] years, respectively (Table 2). However, plot-based estimates can over-emphasise the importance of clusters that might contain a large number of plots, such as the PBDF (Projeto Dinâmica Biológica de Fragmentos Florestais) plots in Manaus (Cluster BDF in Table S1) and the Mount Kinabalu plots in Malaysia (Cluster KIN in Table S1). Minimising this effect by considering each cluster of plots as the sampling unit, the arithmetic mean τ_w was 55 [50, 59] years while the harmonic mean and median values were 48 [44,

Table 2. Summary statistics for woody biomass residence times (τ_w) in 177 tropical forest plots in four continents. Confidence intervals were computed by using a bootstrapping technique (10,000 iterations).

	Arithmetic mean	95% CI	Harmonic mean	95% CI	Median	95% CI
Plot-based analysis						
All plots ($n = 177$)	60	56–64	51	48–54	55	49–60
Africa ($n = 21$)	73	63–84	65	54–75	70	55–92
Americas ($n = 124$)	55	51–59	47	44–50	49	42–56
Asia ($n = 29$)	67	59–79	59	52–67	58	54–68
Australia ($n = 3$)	104	84–121	101	84–116	107	84–121
Cluster-based analysis						
All clusters ($n = 83$)	55	50–59	48	44–51	50	45–57
Africa ($n = 10$)	69	57–83	63	51–76	74	45–90
Americas ($n = 53$)	49	45–55	43	39–47	43	39–51
Asia ($n = 17$)	54	49–59	52	46–57	55	48–63
Australia ($n = 3$)	104	84–121	101	84–116	107	84–121

51] and 50 [45, 57] years, respectively. That the arithmetic mean was greater than the median indicates a positive skew in the distribution of woody biomass residence times in our dataset (Figure 4(a)), which is best described by a three-parameter Weibull distribution function. However, the almost six-fold variation (23–129 years) in woody biomass residence times observed across tropical forest plots in our dataset (Figure 4(a)) suggests that the approach of applying a single τ_w to all tropical forests, as is currently the case for many models, is inappropriate. Focusing on the central tendency of the data also masks the considerable geographical differences that exist in τ_w (Figure 3, Figure 4(c), (d)). For example, τ_w in our Neotropics data (cluster median = 43 [39, 51] years, $n = 53$) were found to be significantly lower (Mann–Whitney U test, $P < 0.01$) than in the Paleotropics (cluster median = 69 [51, 83] years, $n = 30$).

Within regions, interesting trends also emerged. In Amazonia, the tropical region for which most data are available, there were clear geographical differences in woody biomass mean residence time (Figure 3), with plots in western and southern Amazonia generally having much lower τ_w than plots in central and eastern Amazonia. Of the 10 clusters with the lowest τ_w (23–34 years) in our dataset, eight were located in western or southern Amazonia. These include plots (e.g. Kenia and Tanguro) occurring at the extreme end of southern Amazonia, close to the transition to *cerrado* vegetation. Median τ_w of lowland (elevation < 500 m) clusters located in western or southern Amazonia ($n = 27$) was 39 years, median τ_w of clusters of plots in central or eastern Amazonia was 69 years ($n = 15$). Further differences could also be observed across the Paleotropics, with

Asian forests apparently having generally lower τ_w (cluster median of 54 years) than African forests (cluster median of 69 years) and the small number of Australian forests in our database (cluster median of 104 years). In this paper, we focus mainly on large-scale (regional) patterns of variation in woody biomass residence time. Nevertheless, we note that there can also be significant variation at the landscape level too, due to variations in factors such as topography and the associated changes in soil properties (Toledo et al. 2011).

How do climate and elevation influence τ_w ?

In a previous analysis of data on above-ground wood production (W_p) from 104 plots in Amazonia, Malhi et al. (2004) did not find any strong relationships between wood production and climate (average rainfall, average length of the dry season, average incoming radiation flux density), although there was a suggestion of declining wood production with increasing temperature. In addition, Quesada et al. (2012) also found that climate was not generally a strong predictor of geographical variations in stem turnover rates, above-ground biomass and woody productivity across Amazonia – although some effects of dry season and/or mean annual precipitation in reducing W_p and increasing stem turnover rates were noted. Correlation analyses conducted on our pan-tropical dataset generally confirmed the findings of the studies of Malhi et al. (2004) and Quesada et al. (2012) as we could find only weak insignificant correlations (Table S3 in the supplementary material) between τ_w and the climate variables examined (annual rainfall, mean annual temperature). We found, however, that drier

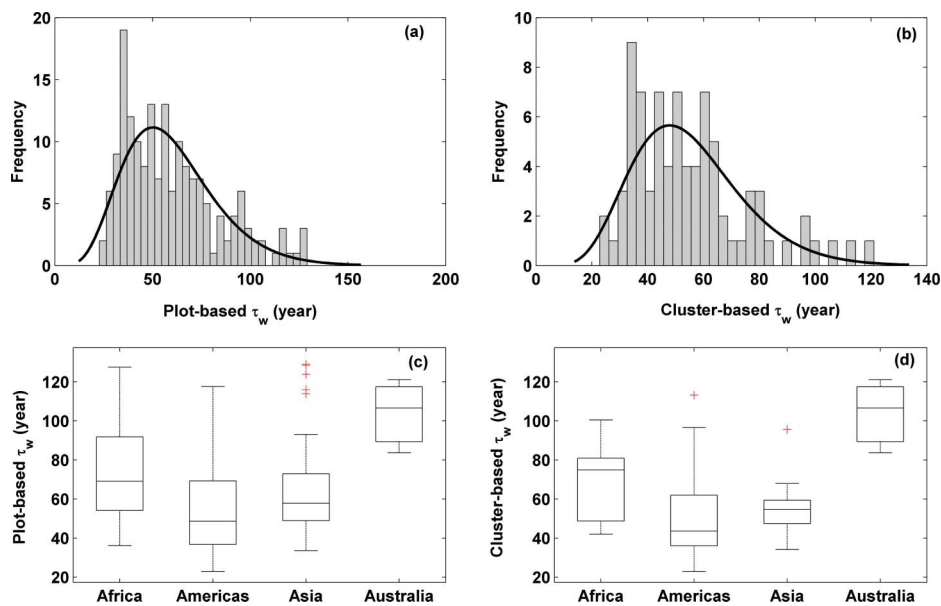


Figure 4. (a) Distribution of plot-based woody biomass residence times (τ_w) in our database ($n = 177$), fully described in Table S1 (available as online supplementary material). (b) Distribution of cluster-based woody biomass residence times in our database ($n = 83$). (c) Box plots illustrating geographical differences in plot-based woody biomass residences ($n = 21$ for Africa, $n = 124$ for the Americas, $n = 29$ for Asia, $n = 3$ for Australia). (d) Box plots illustrating geographical differences in cluster-based woody biomass residence times ($n = 10$ for Africa, $n = 53$ for the Americas, $n = 17$ for Asia, $n = 3$ for Australia). The box encompasses the 25th through 75th percentiles and the horizontal line in the centre of the box indicates the 50th percentile. Red crosses denote outlier points.

forests, such as those located in the southern fringe of Amazonia apparently have low τ_w values compared with wetter forests (Figure 1). The relatively weak relationship of mortality rates and τ_w with climate in tropical forests contrasts with studies in temperate ecosystems where climatic factors (precipitation, maximum and minimum temperatures) have been inferred to be significant drivers in geographical patterns in tree mortality rates (Lines et al. 2010; Dietze and Moorcroft 2011). We also note that strong correlations between large-scale mortality ('blowdown') events and the frequency of heavy rainfall events have also been found, and it has been proposed that the geographical patterns of such blowdown events might help to explain the observed differences in turnover rate between eastern and western Amazonia (Espirito-Santo et al. 2010). However, such blowdown events are likely to be too rare (estimated by Espirito-Santo et al. (2010) to have a recurrence interval of 27,000–90,000 years) to be a major driver of the observed east–west gradient in Amazonian forest tree mortality rates.

A relationship between increasing elevation and τ_w was, however, detectable, this being seen most clearly when individual altitudinal transects were examined separately (Figure 5), thus reducing many of the confounding effects of other variables, such as differences in geological substrates, across sites. In the two Malaysian transects (Kitayama and Aiba 2002), there is clear evidence of increasing τ_w with elevation. In the Peruvian Andes transect (Girardin et al. 2010) the results were less clear, as τ_w increased up to an elevation of ca. 1800 m but declined thereafter to values similar to those observed in the lowland plots in the transect. There was also a suggestion of declining/stabilising woody biomass in the Malaysian plots once a threshold elevation has been reached, although this threshold appears to be at a higher elevation than in the Peruvian plots. Our findings support the conclusions of Moser et al. (2011), who compared a number of tropical altitudinal transect studies and found that there was a general decline in both biomass and productivity with increasing elevation across sites.

How do soil characteristics influence τ_w ?

Soils have previously been shown to exert a strong control on patterns of both above- and below-ground productivity of Amazon forests (Malhi et al. 2004; Aragão et al. 2009; Jiménez et al. 2009; Quesada et al. 2012), and Phillips et al. (2004) found that stem turnover rates in 'richer' soils (e.g. alfisols and basaltic inceptisols) in Amazonia were approximately double those of 'poorer' soils (e.g. oxisols and spodosols). This led to the suggestion that faster turnover in western Amazonia relative to eastern Amazonia may be driven in part by greater soil fertility. Quesada et al. (2012) were able to examine this hypothesis further in the most comprehensive assessment to date of the effects of soil physical and chemical properties on Amazonian forest structure and dynamics. By gathering data on soil physical and chemical properties for 70 Amazonian plots they found strong correlations between different soil phosphorus fractions (readily available P, total extractable P and total P) and W_P , but the strongest correlation for stem turnover rates was with an index of soil physical conditions incorporating factors, such as soil depth, soil structure, topography and drainage capacity.

Are similar relationships between soils and woody biomass residence time observed in the Paleotropics? Here we attempt to answer this question, although it is not possible to answer it as precisely as we would like, given the lack of detailed and methodologically consistent data on soil properties for many paleotropical sites. However, useful insights can potentially be obtained by simple groupings of soils into discrete categories, based on soil type. Such an approach has previously been used when little information other than soil type is available (e.g. Malhi et al. 2004) and in this study we assigned soils into three groupings. Categorisation was based on the pedogenesis spectrum presented by Quesada et al. (2010): (1) relatively young soils (soils younger than Alisols in the WRB classification system), (2) soils of intermediate development stage (e.g. Alisols, Plinthosols and Acrisols in the WRB classification system) and (3) very old, highly weathered soils (e.g. Ferralsols and Podzols in the WRB classification system).

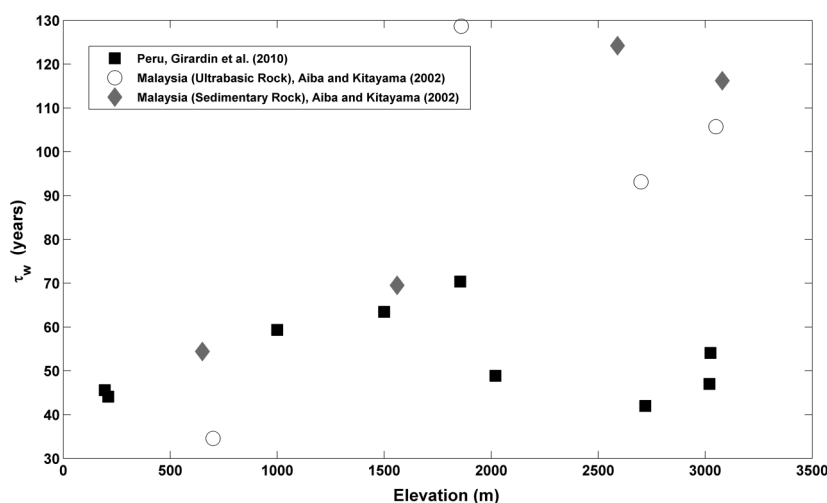


Figure 5. Changes in woody biomass residence time (τ_w) with altitude for three altitudinal transects included in the compiled database.

Taxonomically younger soils tend to present stronger physical constraints for plant function due to their often limited rooting depth and poor structural characteristics (Quesada et al. 2010). There is some relationship between soil pedogenesis stage and soil fertility so that soils at a young stage of pedogenesis (e.g. Cambisols) may be regarded as generally fertile while old soils (e.g. Ferralsols) are generally the least fertile (Quesada et al. 2010). However, soil fertility can vary considerably within an individual soil type. We therefore also devised a second soil categorisation scheme based on soil fertility. The soil pedogenesis and fertility categories assigned to each site in our analysis are shown in Table S2.

The relationship between soil pedogenesis category and τ_w for our dataset can be seen in Figure 6. Significant differences in τ_w were found among soil categories (Kruskal–Wallis test, $P < 0.01$). It is clear from our dataset that there is a definite trend of increasing τ_w with increasing soil age, although this picture is somewhat complicated by the small number of sites on younger soils from the Paleotropics in our dataset. A larger τ_w for strongly weathered soils (e.g. Ferralsols and Podzols) can be seen clearly in both the Neotropical and Paleotropical data and is accentuated when the lowland plots are analysed independently of the highland plots. Very similar results were found when we used fertility categories in our analysis instead of pedogenesis categories. Our results suggest that edaphic factors exert a strong control on woody biomass residence times across all tropical regions, thus strengthening the conclusions of previous studies that found strong correlations between stem turnover rates and soil properties in Amazonia (Quesada et al. 2012).

What are the relationships between τ_w , woody productivity and allocation to stem growth?

We explored the pan-tropical relationship between τ_w and two other important ecosystem variables: above-ground

wood production (W_P) and the proportional allocation of N_P to stem growth. Generally, stronger relationships were found when only the lowland plots were considered than when all plots (lowland and highland) were considered. The steep topography found in many montane transects may provide an additional complicating factor for analysis of τ_w in montane forests. Given the frequent occurrence of landslips and landslides in montane regions, it is not clear whether many montane plots ever achieve anything close to an old-growth biomass equilibrium, thus complicating the estimation of τ_w in these forests. When only lowland forests were considered, however, stronger relationships were observed between τ_w and the other ecosystem variables considered.

The relationship between W_P and τ_w is shown in Figure 7 and can best be described by a power function. The shape of this relationship was found to be very similar in paleotropical forests and neotropical forests (the exponent was ca. -0.5 in both cases), although τ_w was generally higher per unit W_P in paleotropical forests than in neotropical forests. This result can be explained by the fact that the paleotropical forests in our database had a significantly higher biomass than neotropical forests ($342 \pm 6 \text{ t ha}^{-1}$ vs. $282 \pm 2 \text{ t ha}^{-1}$, $P = 0.01$), whereas differences in productivity were not significant ($5.56 \pm 0.13 \text{ t ha}^{-1}$ for the Paleotropics and $5.99 \pm 2.99 \text{ t ha}^{-1}$ for the Neotropics). We note that the published biomass and W_P data used in this study do not take into account the effect of varying tree height. Recent studies (Feldpausch et al. 2011; Banin et al. 2012) have shown that tree height varies considerably across tropical forests, with maximum height of forests in Asia and Africa being on average taller than those in South America. The development of new allometric models which take tree height into account (Feldpausch et al. 2011) will inevitably lead to revised values of the W_P data used in this study, although this should not affect τ_w estimates.

Our results extend the analysis of Malhi et al. (2004), who documented the existence of an inverse

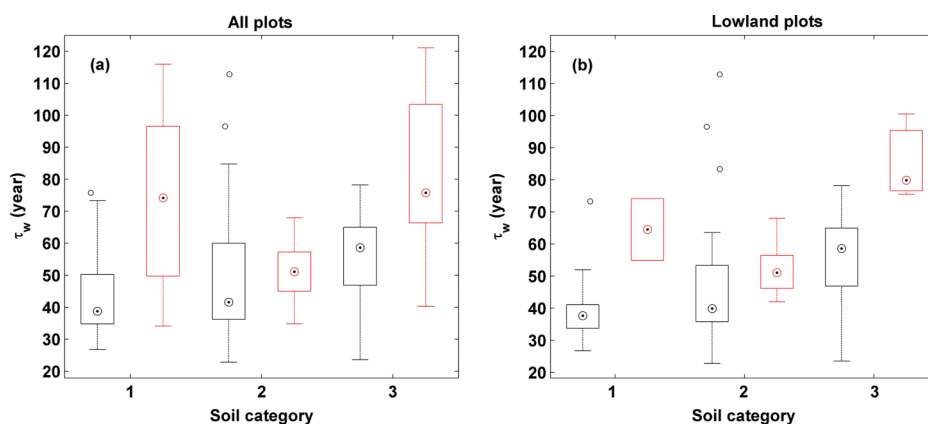


Figure 6. Relationship between woody biomass residence time (τ_w) and soil categories. In this analysis, nearby plots occurring on similar soils have been grouped into clusters. Solid lines denote Neotropical sites while dotted lines denote Paleotropical sites. Soil categories were (1) relatively young soils (soils younger than Alisols in the WRB classification system, $n = 28$ for Neotropics, $n = 5$ for Paleotropics), (2) soils of intermediate development stage (e.g. Alisols, Plinthosols and Acrisols in the WRB classification system, $n = 23$ for Neotropics and $n = 9$ for Paleotropics) and (3) very old, highly weathered soils (e.g. Ferralsols and Podzols in the WRB classification system, $n = 20$ for Neotropics, $n = 11$ for Paleotropics).

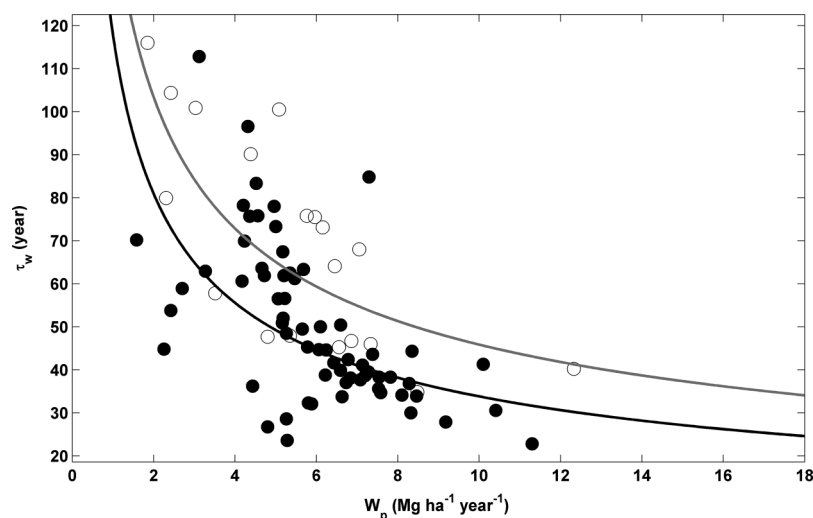


Figure 7. Relationship between woody biomass residence (τ_w) and above-ground woody biomass productivity (W_p). For this analysis, nearby plots occurring on similar soils were grouped into clusters and data for both highland and lowland sites are shown. Open circles denote sites in the Paleotropics ($n = 19$) while closed circles denote sites in the Neotropics ($n = 66$). The grey line is the best fit line for the paleotropical data ($y = 146.66x^{-0.505}$, $r^2 = 0.44$) and the black line is the best fit line for the neotropical data ($y = 117.77x^{-0.542}$, $r^2 = 0.36$).

relationship between woody biomass residence time and woody productivity across Amazonian permanent sampling plots. Similar results have been found in global analyses which related above-ground biomass residence time or stem turnover time to total above-ground N_p (Stephenson and van Mantgem 2005; Keeling and Phillips 2007). Is there a causal mechanistic basis behind the relationship between W_p and τ_w , or is it simply a coincidental correlation? Stephenson et al. (2011) recently addressed this question and presented several hypotheses that might help to explain the correlation between stem mortality and productivity. Along climatic productivity gradients, they argued that an increase in plant enemies might increase mortality rates in warmer and wetter forest regions. Along edaphic productivity gradients, such as the east–west gradient observed in Amazonia, they proposed that mortality rates might reflect the varying abundance of subcanopy trees in forests occurring on soils of different nutrient status. Forests on nutrient-poor soils, they argued, have lower abundance of subcanopy trees and this lowers plot-level mortality rates. In addition, Stephenson et al. (2011) also postulated that growth–defence trade-offs could be important, as slow-growing forests on nutrient-poor soils might also be expected to invest more resources in defence and thus be better protected against plant enemies. These proposed mechanisms therefore suggest that the causes of varying mortality rates across tropical forests are unlikely to be due to a direct effect of W_p . The more important directional control may be that of tree mortality on W_p through its effects on forest size structure and tree density.

We also investigated the relationship between τ_w and the fraction of total N_p allocated to stem growth for sites where full N_p budgets were available. The relationship was clearest for lowland forests, where we found a negative relationship between τ_w and the proportional allocation

to stem growth (Figure 8(a), $r^2 = 0.26$, $P = 0.10$, $n = 11$). Interestingly, the forest in Caxiuanã in eastern Amazonian Brazil deviated somewhat from the best fit line (Figure 7(b)); without this site, the relationship between τ_w and fraction of total N_p allocated to stem growth was considerably stronger ($r^2 = 0.44$, $P = 0.03$). Given the low number of sites for which we had both allocation and τ_w , we treat this result with a degree of caution. Nevertheless, our results do suggest that fast-growing, dynamic forests such as those in much of western Amazonia appear to allocate a greater fraction of their N_p to stem growth than slow-growing forests in eastern Amazonia. We may gain further insight into this result by examining the relationship between the proportional allocation of carbon to stem growth and the absolute woody productivity (W_p), as shown in Figure 8(b). We found a strong, positive relationship, which suggests that differences in proportional allocation to stem growth might help to explain differences across forests in W_p . Given this positive relationship and the negative relationship between W_p and τ_w , it should therefore be expected that a negative relationship should also exist between τ_w and the proportional allocation of N_p to stem growth. This result may at first seem counter-intuitive, but it is important not to confuse N_p allocation with investment in the mechanical strength of wood. It is well known that faster-growing forests in Amazonia have lower wood density than their eastern Amazonian counterparts (Baker et al. 2004). Viewed in terms of classical growth-persistence theory, this would make sense as higher wood density stems might incur lower risk of breakage and hence mortality (King et al. 2006). Stem diameter growth rates, however, are often inversely correlated to wood density (Muller-Landau 2004). Increased allocation of net primary productivity to stem growth relative to foliage production or root production may be

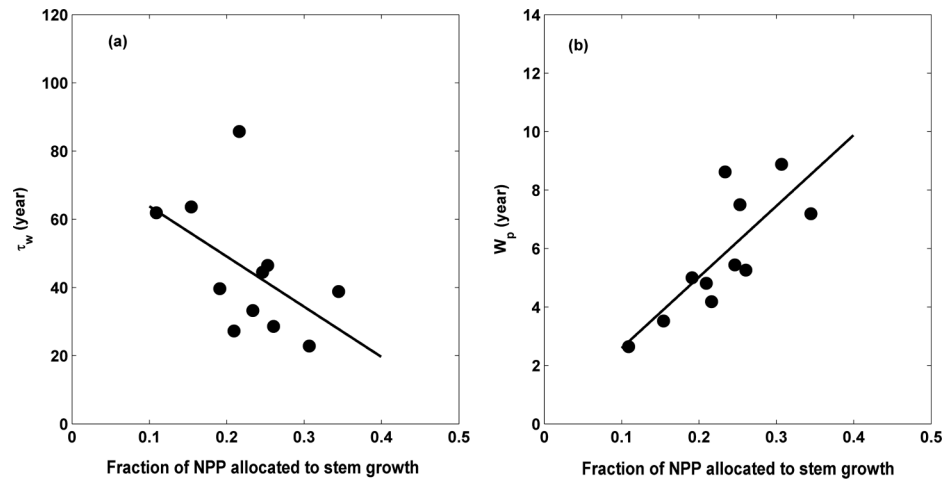


Figure 8. (a) Relationship between woody biomass residence (τ_w) and the fraction of total N_p (sum of wood, canopy and fine root components) allocated to stem wood production for lowland tropical forests where data were available ($n = 11$, $y = 78.57 - 147.28x$, $r^2 = 0.26$, $P = 0.10$). (b) Relationship between W_p and the proportional allocation of NPP to wood ($n = 11$, $y = 12.149x + 0.0783$, $r^2 = 0.66$, $P = 0.01$).

a mechanism for more productive forests to attain faster growth rates.

How well do vegetation models represent woody biomass residence times of tropical forests?

It was possible to obtain default woody biomass residence times for 21 out of 27 models we reviewed, with a large range of τ_w found (Table 2) and with Figure 9(a) showing these default τ_w relative to the tropical forest cluster data distribution ($n = 83$). We were unable to calculate a default woody biomass residence time for some models with dynamic mortality schemes (CLM-DGVM, ED, LPJ, LPJ-GUESS, ORCHIDEE (original version), SEIB-DGVM). A simple test of whether global vegetation models are in fact capturing a ‘typical’ woody biomass residence time of a tropical forest is to assess how close the models are to the central tendency of the data. Although the median woody biomass residence time in the models (ca. 50 years) very closely matched that of the data, there was considerable spread across models in the chosen value of woody biomass residence time. In fact, the range of modelled ‘default’ woody biomass residence times for typical tropical forests was greater than the data range (model range: 20–200 years, data (cluster) range: 23–113 years). Thus the models showed a 10-fold variation in woody biomass residence time of ‘typical’ tropical forests, compared with a six-fold variation across all of the tropical forests in our dataset. Close proximity to the 50th percentile might suggest that a vegetation model is representing the woody biomass residence time of an average tropical forest well. However, the value of the 50th percentile is strongly sensitive to soil age category. The models closest to the 50th percentile of the full dataset were those that assumed a woody biomass residence time of 50 years (CARLUC, GTEC, IBIS (original)). When broken down by soil classification type, however, different models have the best performance.

Biome-BGC, CTEM and LM3v had the best performance for relatively young (category 1) soils, CARLUC, GTEC and IBIS (original) had the best performance for medium aged soils and MOSES-TRIFFID and Hybrid had the best performance for the most highly weathered soils. Perhaps the best measure therefore of a ‘typical’ 50th percentile may be to take the median value of each of the three soil categories considered and weight these by the relative spatial coverage of each category. Based on Vitousek and Sanford (1986), we estimate that 42.6% of tropical soils could be considered to be very infertile soils (category 3), 31.75% could be considered to be moderately infertile (category 2) and 25.65% could be considered to be relatively fertile (category 1). This results in a best estimate of a ‘typical’ τ_w of 59 years.

Nine out of 27 vegetation models reviewed had mortality functions in place of or in addition to background turnover of woody biomass (Table 1): aDGVM, CLM-DGVM, CTEM, ED, Hybrid, LPJ, LPJ-GUESS, ORCHIDEE(original) and SEIB-DGVM. In most cases, mortality was simulated to be induced by a negative carbon balance or by growth inefficiency. Within SEIB-DGVM and LPJ, simple empirical relationships are used to link growth and mortality, the basic premise being that plants are more likely to die when their growth rates are very low. The idea behind the negative carbon balance approach is similar. In the case of ED (Moorcroft et al. 2001), mortality due to negative carbon balance increases exponentially with declining productivity, while in LPJ an entire PFT population is killed if the carbon balance becomes negative over a given year (Sitch et al. 2003). While such approaches could potentially be useful, for example when simulating mortality response to extreme climatic events, they are not capable of simulating spatial variation in mortality processes. Recognising this, Delbart et al. (2010) incorporated the empirical relationship between above-ground woody productivity and woody biomass residence time from Malhi

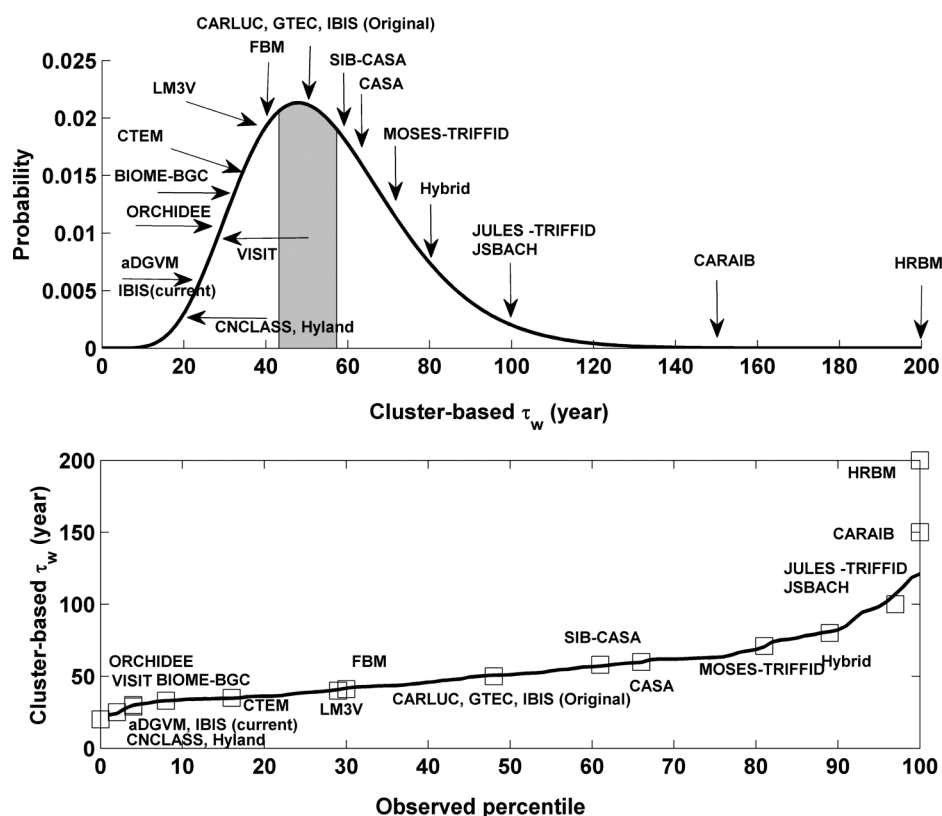


Figure 9. (a) Observed distribution of cluster-based woody biomass residence times (τ_w) (this is the fitted distribution in Figure 4(b)) with arrows overlain showing the default woody biomass residence times in 20 vegetation models which mainly assume a fixed τ_w . In some cases, the models allow τ_w to vary under climatic stress – in these cases we report the baseline (non-stressed) values. The shaded area in the upper panel represents the bootstrapped 95% confidence interval of the median. (b) Values of woody biomass residence time for the dominant tropical forest plant functional type in 22 vegetation models (open squares) superimposed on cluster-based data percentiles which correspond to modelled values.

et al. (2004) for a number of Amazonian plots into the ORCHIDEE model in an attempt to improve the simulated spatial distribution of above-ground biomass in the model. This approach is an improvement on model configurations that assume a fixed τ_w . However, it does not directly consider the main correlate of woody biomass residence time in tropical forests: soils. In many ecosystem models, soils generally only affect above-ground processes through their hydraulic properties which regulate the amount of water available to plants. Some vegetation models now have fully interactive nitrogen cycles (e.g. Zaehle and Friend 2010), but nitrogen is not generally thought to be a limiting nutrient in lowland tropical forests, except for re-growing secondary forests or seasonally dry forests (Davidson et al. 2007). Total soil phosphorus content, on the other hand, has been shown to correlate closely to W_P in Amazonia (Quesada et al. 2012) and has long been considered to be the main nutrient limiting the productivity of most tropical forests (Vitousek 1984). Thus far, only a very small number of modelling studies have attempted to incorporate a phosphorus cycle (Wang et al. 2010; Goll et al. 2012). Furthermore, the relationship between soil physical properties and vegetation dynamics (Quesada et al. 2012) is generally not considered in current ecosystem models.

How will global environmental change affect biomass residence time of tropical forests?

Phillips and Gentry (1994) analysed data from 40 tropical forest plots spanning the period from 1950 to 1990 and found that stem turnover rates increased over this period, with particularly strong increases in the 1980s. This pattern of increasing stem turnover with time was confirmed for a larger number of tropical forest sites distributed across the tropics (Phillips 1996) and subsequently for an even larger number of plots across Amazonia (Phillips et al. 2004). Phillips and Gentry (1994) concluded that “global environmental change was the most likely cause” of the observed increases in stem turnover rates. Of the suite of possible global environmental change drivers, a particularly strong case has been made for the role of increases in atmospheric CO_2 (Lloyd and Farquhar 1996; Lewis et al. 2004b), although the contribution of other potential explanations, such as increasing solar radiation, increased nitrogen deposition due to biomass burning or response to disturbance resulting from extreme climatic events (e.g. droughts) should not be ruled out (Lewis et al. 2009b). Lewis et al. (2004b) explained the observed increase in mortality across tropical forests as follows: (1) increased resource availability (e.g. CO_2) results in an increase in basal area and stem recruitment so that forests increase

both in stem density and the average size of each individual; and (2) these larger/additional trees eventually die, increasing both biomass mortality and stem mortality. This explanation is consistent with the observation that increases in mortality significantly lag increases in growth and recruitment in Amazonia. The lag between these processes is essential for existence of the pan-tropical carbon sink (Chambers et al. 2001).

Mortality rates can in theory increase with no accompanying change in τ_w . For example, if biomass losses are directly proportional to the increase in biomass stocks, there will be no resultant change in τ_w . Without a resultant change in τ_w and assuming no change in allocation, it follows from Equation (1) that a biomass sink should persist as long as there is a stimulation of N_p . However, in a scenario where τ_w decreases, the outcome is very different and the biomass sink is diminished, even assuming no change in the rate of increase of N_p . A decrease in τ_w necessitates a reduction in the average longevity of individual trees. There is no direct evidence at present that increasing CO_2 is reducing the lifetime of tropical forest trees. However, studies on crop systems have shown acceleration of plant lifecycles and earlier onset of death when exposed to higher levels of CO_2 (Kimball et al. 1995). It is difficult, however, to extrapolate such findings to forest ecosystems. A trade-off generally exists, however, across tree species between growth rates and longevity, with faster-growing species usually being shorter lived (e.g. Bugmann and Bigler 2011), although in tropical forests this relationship appears to be much stronger for saplings than for large trees (Wright et al. 2010). Using a forest growth model, Bugmann and Bigler (2011) assumed that the relationship between maximum growth and maximum tree longevity observed across species would hold true under conditions of increasing CO_2 and this effect would offset much of the CO_2 -driven increases in growth in simulations of temperate forest systems. Similar arguments have been made for tropical forests by Körner (2004). However, there is, as yet, no hard evidence that this space-for-time substitution is valid. It is conceivable that increased resource availability may increase mortality rates indirectly as well. For example, the occurrence of lianas has been found to be increasing in tropical forests in recent decades (Phillips et al. 2002). Increasing atmospheric CO_2 concentrations may increase the prevalence of lianas (Schnitzer and Bongers 2011), which in turn may result in increased tree mortality (e.g. Ingwell et al. 2010).

Climate models predict considerable increases in air temperature (3–8 °C) over tropical forests this coming century under the high greenhouse gas emissions pathway that the planet and human society are currently on (Malhi et al. 2009b). A number of models also predict increases in dry season length over Amazonia (Malhi et al. 2009b), with one model predicting extreme reductions (> 50%) in annual precipitation over Amazonia. In the most extreme climate scenarios, the increased drying and increased warming leads to large losses of forest biomass as forests are replaced in the models with other

vegetation types such as shrubs and grasses (Cox et al. 2004). Interestingly, however, the models assessed thus far fail to capture the impacts of drought on above-ground biomass as observed in two throughfall exclusion experiments (Galbraith et al. 2010; Sakaguchi et al. 2011). The MOSES-TRIFFID vegetation model, for example, is the model that results in greatest ‘die-back’ of the Amazon in future simulations but has been found to be very insensitive to rainfall in terms of its biomass response (Galbraith et al. 2010). This is due, at least in part, to the inadequate representation of drought-driven tree mortality in the models. The fixed turnover times assumed by many models introduce lags in the biomass response to drought even though other variables such as G_p or N_p might be greatly reduced under simulated drought conditions (Sakaguchi et al. 2011). There is currently an active debate about the mechanistic basis of drought-driven mortality, especially with regards to the relative importance of hydraulic failure and carbon starvation as causal mechanisms of mortality (Metcalf et al. 2010; McDowell et al. 2011). However, even without a full understanding of the precise mechanisms of drought-driven tree death, there is definite room for improvement on the current default configuration in most models, which simply assume that the woody biomass residence time of plant populations is not directly affected by drought. One possibility would be to apply the relationship of Phillips et al. (2010), which relates increases in tree mortality in tropical forests to cumulative water deficit changes under drought events. However, care must be taken to account for possible changes in species composition which may lessen the impacts of droughts over the longer term, compared with the short-term impacts (Fauset et al. 2012).

Finally, it is important to point out that the simulated impacts of climate change on tropical forests in global vegetation models are largely buffered by the direct effects of increasing atmospheric CO_2 concentrations. Without a large CO_2 fertilisation effect, considerably more forest cover and biomass is lost in global modelling simulations of future climate scenarios (Lapola et al. 2009; Galbraith et al. 2010; Rammig et al. 2010). All of these models assume that biomass residence times will not be directly affected by increasing atmospheric CO_2 – i.e. that growth will be stimulated but there will be no change in average tree lifetimes. This assumption could have significant implications for simulated biomass stocks. If the CO_2 fertilisation response of tropical forest biomass growth in global models is indeed overstated and τ_w decreases under global environmental change, this would mean that future biomass sink strength of tropical forests may ultimately be lower than most models currently suggest.

Acknowledgments

DG, YM and AC were supported by the Gordon and Betty Moore Foundation, through the ‘Amazon-Andes Initiative’ Project. OP is supported by a European Research Council Advanced Grant, ‘Tropical Forests in the Changing Earth System’. We would like to thank Altaf Arain, Nicolas Delbart, Andrew Friend, Hewley Imbuzeiro, Naomi Levine and Hisashi Sato for providing

additional information on the calculation of woody biomass residence time in specific vegetation models. Finally, this work would not have been possible without the data collected and published by the RAINFOR, AFRITRON and CTFS permanent sample plot networks.

Notes on contributors

David Galbraith is a lecturer. His main research interest lies in modelling tropical forest dynamics and biogeochemical cycling.

Yadvinder Malhi is a professor in Ecosystem Science. His research interests focuses on interactions between forest ecosystems and the global atmosphere, with a particular focus on their role in global carbon, energy and water cycles.

Jon Lloyd, Professor, is an expert in tropical forest ecophysiology and has broad research interests in biogeochemical cycling as well as on edaphic modulations of ecosystem structure and function.

Oliver Phillips and Simon Lewis are tropical forest ecologists who coordinate the RAINFOR and AFRITRON plot networks, respectively.

Andrea Castanho and Rosie Fisher are vegetation modellers.

Kofi Affum-Boe, Chris Doughty, Kelvin Peh, Carlos Quesada and Bonaventure Sonké are tropical forest ecologists who all contributed data to this study.

References

- Aragão LEOC, Malhi Y, Metcalfe DB, Silva-Espejo JE, Jimenez E, Navarrete D, Almeida S, Costa ACL, Salinas N, Phillips OL, et al. 2009. Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences* 6:2759–2778.
- Arain MA, Yuan F, Black TA. 2006. Soil-plant nitrogen cycling modulated carbon exchanges in a western temperate conifer forest in Canada. *Agricultural and Forest Meteorology* 140:171–192.
- Arora VK, Boer GJ. 2006. Simulating competition and coexistence between plant functional types in a dynamic vegetation model. *Earth Interactions* 10:1–30.
- Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Higuchi N, Killeen TJ, Laurance SG, et al. 2004. Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 359:353–365.
- Banin L, Feldpausch TR, Phillips OL, Baker TR, Lloyd J, Affum-Boe K, Arets EJMM, Berry NJ, Bradford M, Brien RJW, et al. 2012. What controls tropical forest architecture? Testing environmental, structural and floristic drivers. *Global Ecology and Biogeography* 21:1179–1190.
- Beer C, Reichstein M, Tomelleri E, Ciais P, Jung M, Carvillhais N, Roedenbeck C, Arain MA, Baldocchi D, Bonan GB, et al. 2010. Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science* 329:834–838.
- Bugmann H, Bigler C. 2011. Will the CO₂ fertilization effect in forests be offset by reduced tree longevity? *Oecologia* 165:533–544.
- Chambers JQ, Higuchi N, Tribuzy E, Trumbore S. 2001. Carbon sink for a century. *Nature* 410:429.
- Chambers JQ, Tribuzy ES, Toledo LC, Crispim BF, Higuchi N, dos Santos J, Araujo AC, Kruijt B, Nobre AD, Trumbore SE. 2004. Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecological Applications* 14:S72–S88.
- Chao K-J, Phillips OL, Gloor E, Monteagudo A, Torres-Lezama A, Vasquez Martinez R. 2008. Growth and wood density predict tree mortality in Amazon forests. *Journal of Ecology* 96:281–292.
- Chave J, Condit R, Muller-Landau HC, Thomas SC, Ashton PS, Bunyavejchewin S, Co LL, Dattaraja HS, Davies SJ, Esufali S, et al. 2008. Assessing evidence for a pervasive alteration in tropical tree communities. *PLOS Biology* 6:455–462.
- Chave J, Riera B, Dubois MA. 2001. Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. *Journal of Tropical Ecology* 17:79–96.
- Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J, Holland EA. 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. *Ecological Applications* 11:371–384.
- Clark DB, Mercado LM, Sitch S, Jones CD, Gedney N, Best MJ, Pryor M, Rooney GG, Essery RLH, Blyth E, et al. 2011. The Joint UK Land Environment Simulator (JULES), model description – Part 2: carbon fluxes and vegetation dynamics. *Geoscientific Model Development* 4:701–722.
- Cox PM. 2001. Description of the ‘TRIFFID’ dynamic global vegetation model. Hadley Centre Technical Note 24.
- Cox PM, Betts RA, Collins M, Harris PP, Huntingford C, Jones CD. 2004. Amazonian forest dieback under climate-carbon cycle projections for the 21st century. *Theoretical and Applied Climatology* 78:137–156.
- Davidson EA, de Carvalho CJR, Figueira AM, Ishida FY, Ometto JPHB, Nardoto GB, Saba RT, Hayashi SN, Leal EC, Vieira ICG, et al. 2007. Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. *Nature* 447:995–998.
- Delbart N, Ciais P, Chave J, Viovy N, Malhi Y, Le Toan T. 2010. Mortality as a key driver of the spatial distribution of above-ground biomass in Amazonian forest: results from a dynamic vegetation model. *Biogeosciences* 7:3027–3039.
- Dietze M, Moorcroft PR. 2011. Tree mortality in the eastern and central United States: patterns and drivers. *Global Change Biology* 17:3312–3326.
- Espirito-Santo FD, Keller M, Braswell B, Nelson BW, Froking S, Vicente G. 2010. Storm intensity and old-growth forest disturbances in the Amazon region. *Geophysical Research Letters* 37:L11403.
- Fauset S, Baker TR, Lewis SL, Feldpausch TR, Affum-Boe K, Folli EG, Hamer KC, Swaine MD. 2012. Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. *Ecology Letters* 15:1120–1129.
- Feldpausch TR, Banin L, Phillips OL, Baker TR, Lewis SL, Quesada CA, Affum-Baffoe K, Arets EJMM, Berry NJ, Bird M, et al. 2011. Height-diameter allometry of tropical forest trees. *Biogeosciences* 8:1081–1106.
- Fisher R, McDowell N, Purves D, Moorcroft P, Sitch S, Cox P, Huntingford C, Meir P, Woodward FI. 2010. Assessing uncertainties in a second-generation dynamic vegetation model caused by ecological scale limitations. *New Phytologist* 187:666–681.
- Foley JA, Prentice IC, Ramankutty N, Levis S, Pollard D, Sitch S, Haxeltine A. 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. *Global Biogeochemical Cycles* 10:603–628.
- Friend AD, Stevens AK, Knox RG, Cannell MGR. 1997. A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). *Ecological Modelling* 95:249–287.
- Friend AD and White A. 2000. Evaluation and analysis of a dynamic terrestrial ecosystem model under preindustrial conditions at the global scale. *Global Biogeochemical Cycles* 14:1173–1190.
- Galbraith D, Levy PE, Sitch S, Huntingford C, Cox P, Williams M, Meir P. 2010. Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change. *New Phytologist* 187:647–665.
- Girardin CAJ, Malhi Y, Aragao LEOC, Mamani M, Huasco WH, Durand L, Feeley KJ, Rapp J, Silva-Espejo JE, Silman M, et al. 2010. Net primary productivity allocation and cycling

- of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology* 16:3176–3192.
- Goll DS, Brovkin V, Parida BR, Reick CH, Kattge J, Reich PB, van Bodegom PM and Niinemets U. 2012. Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen and phosphorus cycling. *Biogeosciences* 9:3547–3569.
- Gumpenberger M, Vohland K, Heyder U, Poulter B, Macey K, Rammig A, Popp A, Cramer W. 2010. Predicting pan-tropical climate change induced forest stock gains and losses-implications for REDD. *Environmental Research Letters* 5:014013.
- Hart PJ. 2012. Patterns of tree mortality in a monodominant tropical forest. In: *Tropical forests*, Dr. Padmini Sudarshana, editor. ISBN: 978-953-51-0255-7, InTech. Available from: <http://www.intechopen.com/books/tropical-forests/patterns-of-tree-mortality-in-monodominant-tropical-forests>.
- Hirsch AI, Little WS, Houghton RA, Scott NA, White JD. 2004. The net carbon flux due to deforestation and forest re-growth in the Brazilian Amazon: analysis using a process-based model. *Global Change Biology* 10:908–924.
- Ichii K, Hashimoto H, White MA, Potters C, Hutrya LR, Huete AR, Myneni RB, Nemanis RR. 2007. Constraining rooting depths in tropical forests using satellite data and ecosystem modeling for accurate simulation of gross primary production seasonality. *Global Change Biology* 13:67–77.
- Ingwell LL, Joseph Wright S, Becklund KK, Hubbell SP, Schnitzer SA. 2010. The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *Journal of Ecology* 98:879–887.
- Ise T, Litton CM, Giardina CP, Ito A. 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. *Journal of Geophysical Research-Biogeosciences* 115:G04025.
- Jiménez EM, Moreno FH, Peñuela MC, S. Patiño S, J. Lloyd J. 2009. Fine root dynamics for forests on contrasting soils in the Colombian Amazon. *Biogeosciences* 6:2809–2827.
- Kaduk J, Heimann M. 1996. A prognostic phenology scheme for global terrestrial carbon cycle models. *Climate Research* 6:1–19.
- Keeling HC, Phillips OL. 2007. The global relationship between forest productivity and biomass. *Global Ecology and Biogeography* 16:618–631.
- Kimball BA, Pinter PJ, Garcia RL, LaMorte RL, Wall GW, Hunsaker DJ, Wechsung G, Wechsung F, Kartschall T. 1995. Productivity and water use of wheat under free-air CO₂ enrichment. *Global Change Biology* 1:429–442.
- King DA, Davies SJ, Tan S, Noor NSM. 2006. The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology* 94:670–680.
- Kitayama K, Aiba SI. 2002. Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology* 90:37–51.
- Kohlmaier GH, Brohl H, Siré EO, Plöchl M, Reville R. 1987. Modelling stimulation of plants and ecosystem response to present levels of excess atmospheric CO₂. *Tellus* 39B:155–179.
- Kohlmaier GH, Badeck FW, Otto RD, Hager C, Donges S, Kindermann J, Wurth G, Lang T, Jakel U, Nadler A, et al. 1997. The Frankfurt Biosphere Model: a global process-oriented model of seasonal and long-term CO₂ exchange between terrestrial ecosystems and the atmosphere. 2. Global results for potential vegetation in an assumed equilibrium state. *Climate Research* 8:61–87.
- Körner C. 2004. Through enhanced tree dynamics CO₂ enrichment may cause tropical forests to lose carbon. *Philosophical Transactions of the Royal Society B* 359:493–498.
- Krinner G, Viovy N, de Noblet-Ducoudre N, Ogee J, Polcher J, Friedlingstein P, Ciais P, Sitch S, Prentice IC. 2005. A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. *Global Biogeochemical Cycles* 19:GB1015.
- Lapola DM, Oyama MD, Nobre CA. 2009. Exploring the range of climate biome projections for tropical South America: the role of CO₂ fertilization and seasonality. *Global Biogeochemical Cycles* 23:GB3003.
- Levis S, Bonan GB, Vertenstein M, Oleson KW. 2004. The Community Land Model's Dynamic Global Vegetation Model (CLM-DGVM): technical description and user's guide. NCAR Technical Note.
- Levy PE, Cannell MGR, Friend AD. 2004. Modelling the impact of future changes in climate, CO₂ concentration and land use on natural ecosystems and the terrestrial carbon sink. *Global Environmental Change-Human and Policy Dimensions* 14:21–30.
- Lewis SL, Lloyd J, Sitch S, Mitchard ETA, Laurance WF. 2009b. Changing ecology of tropical forests: evidence and drivers. *Annual Review of Ecology, Evolution and Systematics* 40:520–549.
- Lewis SL, Lopez-Gonzalez G, Sonke B, Affum-Baffoe K, Baker TR, Ojo LO, Phillips OL, Reitsma JM, White L, Comiskey JA, et al. 2009a. Increasing carbon storage in intact African tropical forests. *Nature* 457:1003–1006.
- Lewis SL, Malhi Y, Phillips OL. 2004b. Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society of London B - Biological Sciences* 359:437–452.
- Lewis SL, Phillips OL, Sheil D, Vinceti B, Baker TR, Brown S, Graham AW, Higuchi N, Hilbert DW, Laurance WF, et al. 2004a. Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary. *Journal of Ecology* 92:929–944.
- Lines ER, Coomes DA, Purves DW. 2010. Influences of forest structure, climate and species composition on tree mortality across the Eastern US. *Plos One* 5:e13212.
- Lloyd J. 1999. The CO₂ dependence of photosynthesis, plant growth responses to elevated atmospheric CO₂ concentrations and their interaction with soil nutrient status, II. Temperate and boreal forest productivity and the combined effects of increasing CO₂ concentrations and increasing nitrogen deposition at a global scale. *Functional Ecology* 13:439–459.
- Lloyd J, Farquhar GD. 1996. The CO₂ dependence of photosynthesis, plant growth responses to elevated atmospheric CO₂ concentrations and their interaction with soil nutrient status, I. General principals and forest ecosystems. *Functional Ecology* 10:4–32.
- Malhi Y. 2010. The carbon balance of tropical forest regions, 1990–2005. *Current Opinion in Environmental Sustainability* 2:237–244.
- Malhi Y. 2012. The productivity, metabolism and carbon cycle of tropical forests. *Journal of Ecology* 100:65–75.
- Malhi Y, Aragao L, Galbraith D, Huntingford C, Fisher R, Zelazowski P, Sitch S, McSweeney C, Meir P. 2009b. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon forest. *Proceedings of the National Academy of Sciences of the United States of America* 106:20610–20615.
- Malhi Y, Aragao LEOC, Metcalfe DB, Paiva R, Quesada CA, Almeida S, Anderson L, Brando P, Chambers JQ, da Costa ACL, et al. 2009a. Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Global Change Biology* 15:1255–1274.
- Malhi Y, Baker TR, Phillips OL, Almeida S, Alvarez E, Arroyo L, Chave J, Czimczik CI, Di Fiore A, Higuchi N, et al. 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology* 10:563–591.

- Malhi Y, Doughty C, Galbraith D. 2011. The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society - B* 366:3225–3245.
- Malhi Y, Phillips OL, Lloyd J, Baker T, Wright J, Almeida S, Arroyo L, Frederiksen T, Grace J, Higuchi N, et al. 2002. An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). *Journal of Vegetation Science* 13:439–450.
- McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution* 26:523–532.
- Metcalfe DB, Meir P, Aragao L, Lobo-do-Vale R, Galbraith D, Fisher RA, Chaves MM, Maroco JP, da Costa ACL, de Almeida SS, et al. 2010. Shifts in plant respiration and carbon use efficiency at a large-scale drought experiment in the eastern Amazon. *New Phytologist* 187:608–621.
- Mitchell TD and Jones PD. 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology* 25:693–712.
- Moorcroft PR, Hurtt GC, Pacala SW. 2001. A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecological Monographs* 71:557–585.
- Moser G, Leuschner C, Hertel D, Graefe S, Soethe N, Iost S. 2011. Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment. *Global Change Biology* 17:2211–2226.
- Muller-Landau HC. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* 36:20–32.
- Muller-Landau HC, Condit RS, Chave J, Thomas SC, Bohlman SA, Bunyavejchewin S, Davies S, Foster R, Gunatilleke S, Gunatilleke N, et al. 2006. Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecology Letters* 9:575–588.
- Nir A, Lewis S. 1975. On tracer theory in geophysical systems in the steady and non-steady state. *Tellus* 27B:373–383.
- Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, et al. 2011. A large and persistent carbon sink in the world's forests. *Science* 333:988–993.
- Phillips OL. 1996. Long-term environmental change in tropical forests: increasing tree turnover. *Environmental Conservation* 23:235–248.
- Phillips OL, Aragao L, Lewis SL, Fisher JB, Lloyd J, Lopez-Gonzalez G, Malhi Y, Monteagudo A, Peacock J, Quesada CA, et al. 2009. Drought sensitivity of the Amazon forest. *Science* 323:1344–1347.
- Phillips OL, Baker TR, Arroyo L, Higuchi N, Killeen TJ, Laurance WF, Lewis SL, Lloyd J, Malhi Y, Monteagudo A, et al. 2004. Pattern and process in Amazon tree turnover, 1976–2001. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 359:381–407.
- Phillips OL, Gentry AH. 1994. Increasing turnover through time in tropical forests. *Science* 263:954–958.
- Phillips OL, Lewis SL, Baker TR, Chao KJ, Higuchi N. 2008. The changing Amazon forest. *Philosophical Transactions of the Royal Society B-Biological Sciences* 363:1819–1827.
- Phillips OL, Martinez RV, Arroyo L, Baker TR, Killeen T, Lewis SL, Malhi Y, Mendoza AM, Neill D, Vargas PN, et al. 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* 418:770–774.
- Phillips OL, van der Heijden G, Lewis SL, Lopez-Gonzalez G, Aragao L, Lloyd J, Malhi Y, Monteagudo A, Almeida S, Davila EA, et al. 2010. Drought–mortality relationships for tropical forests. *New Phytologist* 187:631–646.
- Post WM, King AW, Wullschlegel SD. 1997. Historical variations in terrestrial biospheric carbon storage. *Global Biogeochemical Cycles* 11:99–109.
- Prentice I. 2001. The carbon cycle and atmospheric carbon dioxide. In: Houghton J, editor. *Climate change 2001: the scientific basis: contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge (UK): Cambridge University Press. p. 183–237.
- Quesada CA, Lloyd J, Schwarz M, Patino S, Baker TR, Czimczik C, Fyllas NM, Martinelli L, Nardoto GB, Schmerler J, et al. 2010. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences* 7:1515–1541.
- Quesada CA, Phillips OL, Schwarz M, Czimczik CI, Baker TR, Patiño S, Fyllas NM, Hodnett MG, Herrera R, Almeida S, et al. 2012. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* 9:2203–2246.
- Rammig A, Jupp T, Thonicke K, Tietjen B, Heinke J, Ostberg S, Lucht W, Cramer W, Cox P. 2010. Estimating the risk of Amazonian forest dieback. *New Phytologist* 187: 694–706.
- Roy J, Saugier B. 2001. Terrestrial primary production: definitions and milestones. In: Roy J, Mooney HA, Saugier B, editors. *Terrestrial global productivity*. San Diego (CA): Academic Press. p. 1–6.
- Saatchi SS, Harris NL, Brown S, Lefsky M, Mitchard ETA, Saleska SR, Zutta BR, Buermann W, Lewis SL, Hagen S, et al. 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences of the United States of America* 108: 9899–9904.
- Sakaguchi K, Zeng X, Christoffersen BJ, Restrepo-Coupe N, Saleska SR, Brando PM. 2011. Natural and drought scenarios in an east central Amazon forest: fidelity of the Community Land Model 3.5 with three biogeochemical models. *Journal of Geophysical Research-Biogeosciences* 116: G011029.
- Sato H. 2009. Simulation of the vegetation structure and function in a Malaysian tropical rain forest using the individual-based dynamic vegetation model SEIB-DGVM. *Forest Ecology and Management* 257:2277–2286.
- Sato H, Itoh A, Kohyama T. 2007. SEIB-DGVM: A new dynamic global vegetation model using a spatially explicit individual-based approach. *Ecological Modelling* 200:279–307.
- Schaefer K, Collatz GJ, Tans P, Denning AS, Baker I, Berry J, Prihodko L, Suits N, Philpott A. 2008. Combined Simple Biosphere/Carnegie-Ames-Stanford Approach terrestrial carbon cycle model. *Journal of Geophysical Research-Biogeosciences* 113:G03034.
- Scheiter S, Higgins SI. 2009. Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach. *Global Change Biology* 15:2224–2246.
- Schnitzer SA, Bongers F. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters* 14:397–406.
- Sheil D, May RM. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* 84:91–100.
- Shevliakova E, Pacala SW, Malyshev S, Hurtt GC, Milly PCD, Caspersen JP, Sentman LT, Fisk JP, Wirth C, Crevoisier C. 2009. Carbon cycling under 300 years of land use change: importance of the secondary vegetation sink. *Global Biogeochemical Cycles* 23:GB2022.
- Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan JO, Levis S, Lucht W, Sykes MT, et al. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* 9:161–185.
- Smith B, Prentice IC, Sykes MT. 2001. Representation of vegetation dynamics in the modelling of terrestrial

- ecosystems: comparing two contrasting approaches within European climate space. *Global Ecology and Biogeography* 10:621–637.
- Stephenson NL, van Mantgem PJ. 2005. Forest turnover rates follow global and regional patterns of productivity. *Ecology Letters* 8:524–531.
- Stephenson N, van Mantgem P, Bunn A, Bruner H, Harmon M, O'Connell K, Urban D, Franklin J. 2011. Causes and implications of the correlation between forest productivity and tree mortality rates. *Ecological Monographs* 81: 527–555.
- Toledo JJ, Magnusson WE, Castilho C. 2011. Tree mode of death in Central Amazonia: effect of soil and topography on tree mortality associated with storm disturbances. *Forest Ecology and Management* 263:255–261.
- Vanclay JK. 1991. Mortality functions for north Queensland rain forests. *Journal of Tropical Forest Science* 4:15–36.
- Vieira S, Trumbore S, Camargo PB, Selhorst D, Chambers JQ, Higuchi N, Martinelli LA. 2005. Slow growth rates of Amazonian trees: consequences for carbon cycling. *Proceedings of the National Academy of Sciences* 102: 18502–18507.
- Vitousek PM. 1984. Litterfall, nutrient cycling and nutrient limitation in tropical forests. *Ecology* 65:285–298.
- Vitousek PM, Sanford RL. 1986. Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* 17:137–167.
- Wang YP, Law RM, Pak B. 2010. A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. *Biogeosciences* 7:2261–2282.
- Warnant P, Francois L, Strivay D, Gerard JC. 1994. CARAIB - A global model of terrestrial biological productivity. *Global Biogeochemical Cycles* 8:255–270.
- Wolf A, Ciais P, Bellassen V, Delbart N, Field CB, Berry JA. 2011. Forest biomass allometry in global land surface models. *Global Biogeochemical Cycles* 25:GB3015.
- Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling JW, Davies SJ, Diaz S, et al. 2010. Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* 91:3664–3674.
- Zaehle S, Friend AD. 2010. Carbon and nitrogen cycle dynamics in the O-CN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates. *Global Biogeochemical Cycles*, 24, GB1005, doi:10.1029/2009GB003521.
- Zhao MS, Running SW. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science* 329:940–943.