Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2011) ••, ••–••

Global Ecology and Biogeography
A Journal of Macroecology

RESEARCH PAPER

Temperature explains global variation in biomass among humid old-growth forests

Markku Larjavaara[1,2]* and Helene C. Muller-Landau[1]

[1]*Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Panama, Republic of Panama,* [2]*Department of Forest Sciences, PO Box 27, FI-00014 University of Helsinki, Finland*

*Correspondence: Markku Larjavaara, Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Panama, Republic of Panama.
E-mail: markku.larjavaara@gmail.com

ABSTRACT

Aim To develop and test a simple climate-based ecophysiological model of aboveground biomass – an approach that can be applied directly to predicting the effects of climate change on forest carbon stores.

Location Humid lowland forests world-wide.

Methods We developed a new approach to modelling the aboveground biomass of old-growth forest (AGB_{max}) based on the influences of temperature on gross primary productivity (GPP) and what we call total maintenance cost (TMC), which includes autotrophic respiration as well as leaf, stem and other plant construction required to maintain biomass. We parameterized the models with measured carbon fluxes and tested them by comparing predicted AGB_{max} with measured AGB for another 109 old-growth sites.

Results Our models explained 57% of the variation in GPP across 95 sites and 79% of the variation in TMC across 17 sites. According to the best-fit models, the ratio of GPP to maintenance cost per unit biomass (MCB) peaks at 16.5 °C, indicating that this is the air temperature leading to the highest possible AGB_{max} when temperatures are constant. Seasonal temperature variation generally reduces predicted AGB_{max}, and thus maritime temperate climates are predicted to have the highest AGB_{max}. The shift in temperatures from temperate maritime to tropical climates increases MCB more than GPP, and thus decreases AGB_{max}. Overall, our model explains exactly 50% of the variation in AGB among humid lowland old-growth forests.

Main conclusions Temperature plays an important role in explaining global variation in biomass among humid lowland old-growth forests, a role that can be understood in terms of the dual effects of temperature on GPP and TMC. Our simple model captures these influences, and could be an important tool for predicting the effects of climate change on forest carbon stores.

Keywords
Carbon stocks, climate change, ecosystem respiration, gross primary productivity (GPP), humid forests, maintenance cost, net primary productivity (NPP), temperature sensitivity.

INTRODUCTION

Forests around the world vary tremendously in the sizes of trees and thus in their aboveground biomass (AGB). People have long marvelled at the exceptionally large trees of certain regions such as western coastal North America, and sought to understand why such large trees are found in these areas and not others. Temperature and rainfall, and their seasonal patterns, are clearly important factors, and are the basis for phenomenological models of forest type, such as those that define biomes (Rumney, 1968). These models are useful in summarizing patterns, but provide limited insights into the underlying processes, and at best a weak basis for generalizing to novel climate regimes expected under global climate change. Atmospheric and climate change are hypothesized to be changing AGB and thereby global forest carbon stores (Phillips *et al*., 1998; Myneni *et al*., 2001;

DOI: 10.1111/j.1466-8238.2011.00740.x
http://wileyonlinelibrary.com/journal/geb

Chave, 2008; Lewis *et al.*, 2009), but the mechanisms, direction and magnitude of such changes continue to be a subject of intense debate (Wright, 2005). Models that capture the contribution of spatial variation in climate to spatial variation in forest carbon stores in extant forests could provide important insights into how changing climates will affect forest carbon stores in the long term.

Spatial variation in forest AGB has been related to climate in a number of previous studies. Climate explains a small proportion of AGB variation in regional studies of tropical forests in the Amazon (Malhi *et al.*, 2006) and Borneo (Slik *et al.*, 2010). The climate effects are similar in both regions with high annual precipitation and low seasonality associated with high AGB. However, the non-climatic effects are contradictory as wood density was a significant positive correlate of AGB in the Amazon but not in Borneo, and soil fertility in Borneo but not in the Amazon. Along elevational gradients within the tropics, AGB declines as elevation increases (Kitayama & Aiba, 2002; Raich *et al.*, 2006), a pattern Raich *et al.* (2006) attributed to the decline in temperature. However, many other factors also change with elevation and could confound these results, including solar insolation (cloudiness), air pressure (which can directly affect photosynthesis; see Gale, 1972), slope, soil stability and species richness. On global scales, AGB does not generally increase with temperature, as the highest AGB is found in some moist temperate forests, though there is tremendous variation in AGB among moist temperate forests (Keith *et al.*, 2009). In an analysis of 276 forest plots of 0.1 ha in the Americas, Stegen *et al.* (2011) found that AGB was inversely related to mean annual temperature among wet tropical forest sites and positively related among moist tropical forests, and that annual precipitation was positively related to biomass in both temperate forests and dry tropical forests. All relationships were weak, but this could be due in part to the small plot size and associated sampling error. Stegen *et al.* (2011) noted that forest biomass in these plots was highly correlated with the size of the largest tree (a result that may in part reflect their small plot size), and concluded that climatically variable hydraulic limitations on tree size are important in driving variation in forest biomass. Specifically, they suggested that high AGB forests are not found in dry climates because of hydraulic limits on water transportation in individual trees, while other factors determine AGB in moist climates.

By definition, old-growth forest biomass is the biomass at which gains from tree growth and recruitment are balanced by losses due to the deaths of trees and parts of trees. It has long been thought that high productivity leads to higher biomass, and this idea was supported by some older studies (reviewed by Keeling & Phillips, 2007). However, when tropical plots are included it becomes evident that net primary productivity (NPP) is not correlated with AGB: the highest AGB is found in moist temperate forests with intermediate NPP, and the highest NPP in tropical forests with intermediate AGB (Keeling & Phillips, 2007). Certainly, increases in NPP would be expected to lead to proportional increases in old-growth forest biomass if the proportion of biomass lost to mortality (of trees, branches and leaves), henceforth the turnover rate, were unchanged. But clearly, this is not the case, and efforts to understand old-growth forest biomass mechanistically must consider more than just productivity. Unfortunately, though above-ground NPP can be measured relatively easily and modelled based on climate, turnover rates depend not only on extrinsic factors but also strongly on the life-history strategies of trees, making it difficult to develop mechanistic models for turnover from abiotic site characteristics.

Our approach is to focus instead on the balance of total carbon revenue of plants, or gross primary productivity (GPP), versus total plant carbon expenditures on the maintenance plant biomass, which we refer to as total maintenance cost (TMC). There are various advantages to working with GPP and TMC rather than NPP and turnover. Climate drives photosynthesis and therefore GPP of closed-canopy forests more directly than NPP, as there is neither biological rationale nor empirical evidence for a constant ratio of NPP to GPP (Zhang *et al.*, 2009). Furthermore, the ratio of NPP to GPP decreases during succession as larger tree trunks require more autotrophic respiration, while GPP is relatively constant after canopy closure (Mäkelä & Valentine, 2001). GPP can be estimated with eddy-covariance methods (Baldocchi, 2008) or from remote sensing (Jahan & Gan, 2009) or climate (Beer *et al.*, 2010). Finally, it is relatively easier to model the effect of climate on TMC than on turnover, because TMC is composed not only of those turnover rates that are difficult to model (including both tree mortality and regular replacement of tree parts, e.g. leaves), but also of autotrophic respiration, the temperature sensitivity of which has been studied in depth.

Here, we present our novel GPP- and TMC-based approach to modelling the above-ground biomass of old-growth forest (AGB_{max}), parameterize the GPP and TMC models, and test them by comparing predicted AGB_{max} to measured AGB in 109 humid old-growth sites around the world. Our models do not consider the impacts of water stress, fire and browsing, impacts that are common in arid climates and which are difficult to model (Sankaran *et al.*, 2005), nor do they include low air pressure, steep slopes and low species diversity that affect biomass at high elevations. Thus, we restrict our modelling and analyses to humid, lowland areas, areas that encompass a majority of the world's forests.

METHODS

GPP model

Our GPP model for humid, lowland forests is based in large part on simple functional forms from the literature. We assumed GPP is a function of sun elevation, θ, temperature, T, and the difference in mean temperature from the previous month, ΔT.

In the absence of atmospheric diffraction, the amount of solar radiation arriving per unit area would be proportional to the sine of sun elevation ($\sin\theta$). However GPP is not proportional to energy arriving per unit area (Pallardy, 2008) because photosynthetic rates asymptote at sufficiently high radiation (Pallardy,

2008) and because diffuse radiation is used more efficiently than direct radiation (Gu *et al.*, 2002) and the proportion of diffuse radiation depends on sun elevation (Spitters *et al.*, 1986). Therefore we assumed that GPP increases as a power function of sin θ, and chose the exponent 0.7 based on eddy-covariance data from Hyytiälä, Finland (P. Kolari, pers. comm.).

We modelled the influence of temperature on GPP as a unimodal function that dropped to zero at temperatures below $T_{\min}$ or above $T_{\max}$, and was proportional to $(T - T_{\min})^2(T_{\max} - T)$ at intermediate temperatures (Lenton & Huntingford, 2003). Inhibition of photosynthesis at high and at low temperatures has multiple causes, and the general pattern of a slow rise and rapid decline with rising temperature is well established (Pallardy, 2008).

Effects of changes in temperature on plants via acclimation of plant energetics are complex (Pallardy, 2008). Since the available data were on monthly rather than daily time-scales, we assumed that the penalty of acclimation for GPP is proportional to the absolute difference in mean temperature from the previous month (Mäkelä *et al.*, 2008). Combining these factors, our equation for GPP is thus

$$\mathrm{GPP}(\theta, T, \Delta T) = \begin{cases} g(\sin\theta)^{0.7}(T - T_{\min})^2 & \theta > 0 \text{ and} \\ (T_{\max} - T)(1 - m|\Delta T|), & T_{\min} < T < T_{\max}, \\ 0 & \text{otherwise} \end{cases} \tag{1}$$

where g, $T_{\min}$, $T_{\max}$, and m are fitted parameters ($T_{\min}$ and $T_{\max}$ are the lower and upper bounds on the temperatures at which photosynthesis can occur). Note that under this model GPP does not depend on biomass, as we restrict our attention to forests after canopy closure, after which both leaf area index (LAI) and GPP become relatively constant (Goulden *et al.*, 2011) (though hydraulic limitation can lead to reductions in GPP for very tall trees; Ryan *et al.*, 2004).

Maintenance cost and AGB models

Like the model for GPP, our model for maintenance costs for the most part follows simple functional forms found in the literature. We assumed that TMC is influenced by temperature, T, difference in mean temperature from the previous month, ΔT, and AGB. Since the influence of temperature on turnover is not well known we assumed the autotrophic respiration component of TMC dominated the temperature–TMC relationship and assumed a Q_{10} function (Ryan, 1991), as this is the dominant approach to representing the temperature sensitivity of respiration (Mahecha *et al.*, 2010). In the same way as with GPP we assumed that the penalty of acclimation is proportional to the absolute difference in mean temperature from the previous month. We further modelled maintenance cost as a power function of AGB (Mori *et al.*, 2010). In total, we modelled TMC as

$$\mathrm{TMC}(\mathrm{AGB}, T, \Delta T) = ch^{T/10}(1 + k|\Delta T|)\,\mathrm{AGB}^b \tag{2}$$

where c, h, k and b are fitted parameters.

From these equations, we were able then to predict $\mathrm{AGB}_{\max}$, the maximum AGB that can be supported for a given climate and latitude. To do this, it is useful to first define what we call maintenance cost per unit biomass (MCB) as

$$\mathrm{MCB} = \frac{\mathrm{TMC}}{\mathrm{AGB}^b} = ch^{T/10}(1 + k|\Delta T|) \tag{3}$$

Then the AGB at which TMC equals GPP, $\mathrm{AGB}_{\max}$, is

$$\mathrm{AGB}_{\max}(\boldsymbol{\theta}, \boldsymbol{T}, \Delta\boldsymbol{T}) = \left(\frac{\sum \mathrm{GPP}(\boldsymbol{\theta}, \boldsymbol{T}, \Delta\boldsymbol{T})}{\sum \mathrm{MCB}(\boldsymbol{T}, \Delta\boldsymbol{T})} \right)^{1/b} \tag{4}$$

where $\boldsymbol{\theta}$, $\boldsymbol{T}$ and $\Delta\boldsymbol{T}$ are vectors encompassing intra-annual variation in sun elevation and temperature. Thus, $\mathrm{AGB}_{\max}$ peaks where the ratio of annual GPP to annual MCB peaks. Note that the location of this peak is independent of the fitted parameters g and c, and depends only on the other six parameters.

Parameterization

We parameterized the models for GPP and TMC of humid, lowland old-growth forest from global datasets. We used average monthly temperature and average monthly diurnal temperature variation interpolated to the closest 10′ latitude–longitude intersection based on data from meteorological stations, recorded mostly between 1961 and 1990 (New *et al.*, 2002). We used measurements of forest carbon budgets (Luyssaert *et al.*, 2007) to fit GPP and TMC.

Sites were included in the parameterization of the GPP and TMC models, and in the evaluation of the predicted $\mathrm{AGB}_{\max}$, only if they met specific criteria determined a priori. Due to the direct influence of water stress on GPP (Pallardy, 2008) and indirect impacts via fire regimes and life-history strategies, effects that are beyond the scope of the current model, we excluded sites in which annual potential evapotranspiration (Thornthwaite, 1948) exceeds precipitation (New *et al.*, 2002) (Note, however, that the estimates of annual potential evapotranspiration that we used are potentially subject to bias; see Fisher *et al.*, 2011.) We excluded sites at altitudes above 1000 m (altitude from New *et al.*, 2002) due to the direct impact of air pressure on photosynthesis (Gale, 1972) and potentially depauperate tree species communities. For the same reasons of isolation and potentially depauperate communities, we excluded sites on islands that had never been connected to continents. In addition, we had to exclude two sites on a small island (Hawaii) for which climate data (New *et al.*, 2002) were unavailable (this influences only the part of the sensitivity analysis in which oceanic islands are included) and we had to move one coastal site (Spain) to the closest 10′ latitude–longitude intersection on land as interpolated climate data were available only over land (New *et al.*, 2002).

We assigned an uncertainty class to each measurement based on both the verbal description of the stand structure and history and the field methodology reported in the database (‘GPP_method’). For the parameterization of the GPP model (equation 1), we aimed to use only closed-canopy sites, and therefore excluded sites with time since a major disturbance of less than 6 years (3 years in the tropics) and all fruit plantations. Each of the remaining sites was assigned an uncertainty class between 1 and 3. All sites began with uncertainty classes of 1; an additional point was added for sites whose uncertainty scores in Luyssaert's database (Luyssaert *et al*., 2007) were above 0.5, and a point was added if there was mention of a major disturbance such as thinning but lack of information on its timing. We excluded sites with uncertainty class 3, leaving 95 sites for the GPP fits. In most cases, these GPP data were based on eddy-covariance measurements.

For the parameterization of the TMC model (equation 2), we used old-growth forest sites for which both GPP and AGB data were available. We used GPP data to parameterize the TMC model under the assumption that annual TMC should equal annual GPP in old-growth forests, and because GPP data were available for more sites and are considered more accurate. We excluded all sites with a 'management code' other than 'UM' (unmanaged) and time since a major disturbance of less than 60 years (30 years in the tropics). These threshold ages reflect a compromise necessitated by the dearth of data for very old forests, and the need for an adequate sample size for reasonable model parameterization. We recognize that biomass accumulation clearly continues beyond 60 years (or 30 years in the tropics), though at a fairly slow rate, and that the inclusion of older successional forests in this analysis is likely to cause a small bias towards overestimating TMC for a given biomass, and thus underestimating expected AGB_{max}; unfortunately, currently available data do not permit a better alternative approach. As before, each site was assigned an uncertainty class, starting with a default value of 1. A reported uncertainty score above 0.5 (Luyssaert *et al*., 2007) and time since a major disturbance of 60–120 years (30–60 years in the tropics) both increased our uncertainty class by one point. We excluded sites with uncertainty class of 3 (none) and thus used data from 17 sites.

Several stands had data from multiple years or from several GPP measurement methods in the same year. For both TMC and GPP we used only one data point per site, averaging over the data rows for the lowest available uncertainty class. Both models were fitted by ordinary least squares on log-transformed annual values [equivalent to minimizing the root mean squared error (RMSE) in log-transformed values]. Searches for the best parameter values were done using a quasi-Newtonian method of hill-climbing optimization modified to allow box constraints, as implemented in the R package (Development-Core-Team, 2008) under the *optim* function with method = 'L-BFGS-B' (Byrd *et al*., 1995). To calculate annual GPP or TMC for a given set of monthly temperature means and diurnal ranges, we calculated temperature and sun elevation at 30-min intervals for mid-month days, and then did a weighted sum over months, weighting by average days per month.

We restricted parameter values a priori to ranges considered realistic based on the literature (Pallardy, 2008). We set the range of T_{min} from −5 to 5 (Pallardy, 2008), of T_{max} from 40 to 50 (Pallardy, 2008), and of m from 0 to 0.05 (so that GPP remains positive even with the maximal ΔT of 18.8 °C in the data). Because k and m have parallel roles in the effects of acclimation on GPP and TMC, we set the range of k to be equal to that of m, thus extending from 0 to 0.05. We allowed a wide range of possible values for h from 1.5 to 3.0, taking into consideration that MCB includes not only autotrophic respiration but also construction of leaves, roots and other plant material to balance losses (Pallardy, 2008). We set the upper bound of b to be equal to 0.8, the scaling exponent of autotrophic respiration for trees including large individuals (Mori *et al*., 2010). If TMC were dominated by construction of leaves and fine roots, it would be likely to scale roughly to AGB and because in old-growth forests autotrophic respiration is likely to dominate the relation we placed the lower bound of b half way between zero and the maximum, i.e. to 0.4. We calculated the sun elevation based on a sinusoidal annual and diurnal cycle (modified from Forsythe *et al*., 1995). We assumed air temperature (T) peaked 4 h after solar noon. The coefficients c and g were effectively unrestricted; nominal bounds were set at $\exp(-100)$ and $\exp(100)$, and fitted parameters never approached these bounds.

Both equations were fitted to annual data; expected values were computed by summing over seasonal and diurnal variation in sun elevation, temperature and temperature differences from the previous month.

Evaluation

To evaluate the model, we compared the AGB_{max} calculated from intra-annual patterns of temperature and sun elevation to observed AGB at humid, lowland old-growth sites. We calculated predicted AGB_{max} for a given set of monthly temperatures and sun elevations by first calculating expected annual GPP and MCB based on the fitted models, following equation 4. We obtained the observed AGB from two datasets (Chave, 2008; Keith *et al*., 2009) that together cover all major forest regions of the world, but that over-represent areas famous for high AGB, such as the north-western United States and south-western Australia.

We applied the same data filtering criteria in the evaluation as in the parameterization: we excluded sites that were at high elevation (> 1000 m), were arid (potential evapotranspiration > precipitation) or were oceanic islands. In addition there were six sites (five in Venezuela and one in Costa Rica) for which both temperatures and precipitation (and in some cases altitude) reported for the location in Keith *et al*. (2009) differed drastically from those interpolated in New *et al*. (2002), calling into question the accuracy of the location data and/or the relevance of the interpolated climate data. One site had to be excluded as it was on a small island (American Samoa) for which climate data (New *et al*., 2002) were not available (because it was on an oceanic island, this exclusion influences only the sensitivity analysis). We moved one coastal site to the closest 10′ latitude–longitude intersection on land as interpolated climate data were available only over land (New *et al*., 2002). This left us with 109 old-growth sites for the evaluation.

We evaluated the sensitivity of the results by varying four fixed model parameters, ten values at which parameters were bounded, and five data selection criteria, varying one factor at a time. The four fixed parameters were the exponent on sin θ in equation 1, the exponent on $(T - T_{min})$ in equation 1, the exponent on $(T_{max} - T)$ in equation 1 and the lag between solar noon and peak temperature. The 10 bounds were the lower and upper bounds for T_{min}, T_{max}, h and b, and the upper bounds for the acclimation parameters m and k. The lower bound of both acclimation parameters was zero, and this was not varied (negative values would be nonsensical). The five data selection criteria were the maximum altitude for inclusion, the island exclusion criterion, the potential evapotranspiration versus precipitation criterion, the data uncertainty criterion for TMC and the data uncertainty criterion for GPP.

We developed all the models, and planned the parameterization and sensitivity analysis fully before computations, and did not change data selection criteria or model characteristics based on results (i.e. no 'tuning'). Appendix S1 in the Supporting Information contains all the data, which as noted previously are drawn from the original publications (New *et al.*, 2002; Luyssaert *et al.*, 2007; Chave, 2008; Keith *et al.*, 2009).

RESULTS

The best-fit functions explained 57% of the variation in GPP among 95 humid, lowland sites (Fig. 1a), and 79% of the variation in TMC among 17 sites (Fig. 1b). Best-fit parameter values were: $g = 3.6 \times\cdot 10^{-5}$; $T_{min} = -5°C$; $T_{max} = 40°C$; m = 0.05; c = 4.8×10^{-3}; $h = 1.7$; $k = 0.05$; $b = 0.4$.

Under the fitted models, GPP peaks at 25 °C, with a steep decline at higher temperatures, while MCB and TMC increase continuously and exponentially (Fig. 2a). These relationships in combination lead to the prediction that the ratio of GPP to MCB, and therefore AGB_{max}, peaks at a mean annual temperature of 16.5 °C in the absence of seasonal or diurnal temperature variation (New *et al.*, 2002) (Fig. 2b). Though the curve for predicted AGB_{max} versus temperature is relatively symmetric, the deficit of GPP relative to TMC is greater for higher temperatures (Fig. 2a). Therefore, a heat wave of 32.5 °C is several times more energetically costly to an old-growth forest than a cold snap of 0.5 °C. Under conditions where TMC is small relative to GPP, such as in young stands, we would expect maximal rates of biomass accumulation to occur at temperatures close to the peak of GPP, 25 °C.

Seasonal temperature variation generally reduces predicted AGB_{max} (Fig. 3). The decline in AGB_{max} with increasing seasonality is especially strong for average annual temperatures between 10 and 20 °C. In contrast, at the lowest average annual temperatures, below about 5 °C, increased seasonality leads to increases in AGB_{max}. The effects of changes in average annual temperature also differ depending on seasonality. A decrease in average annual temperature at temperatures below 16.5 °C lowers AGB_{max} much more when there is low seasonality than when there is high seasonality, consistent with observed trends in Eurasia and North America (as reflected in forest height Lefsky, 2010).

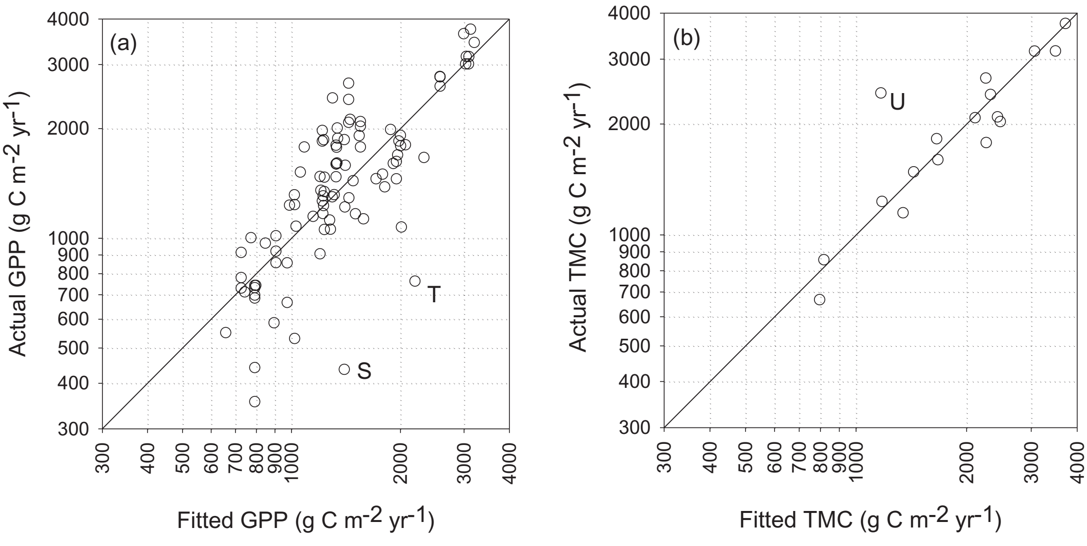

Figure 1 Expected gross primary productivity (GPP) under the best-fit model plotted against measured GPP (a), and expected total maintenance cost (TMC) under the best-fit model plotted against measured TMC (b), relative to the 1:1 line (solid). The outlying data point marked S (panel a) represents a 3-year-old *Pseudotsuga menziesii* stand (Humphreys *et al.*, 2006) which was wrongly included in the parameterization because the recent clear-cut was not reflected in the 'management' field (Luyssaert *et al.*, 2007). We did not exclude it *post hoc* as the contradictory information was revealed only by additional checks performed for outlying data points. Point T (panel a) represents a *Quercus* stand in Portugal, included in our parameterization as the annual precipitation was estimated to be on average 688 mm (New *et al.*, 2002) and therefore exceeds potential evapotranspiration of 589 mm. However, in 2004, the year for which GPP data are available, the measured precipitation was only 488 mm (Luyssaert *et al.*, 2007). Point U (panel b) represents a 60-year-old nitrogen-fixing *Alnus glutinosa* stand in northern Germany; note that 60 years is the minimum age for inclusion as an old-growth forest in this analysis (Kutsch *et al.*, 2001).

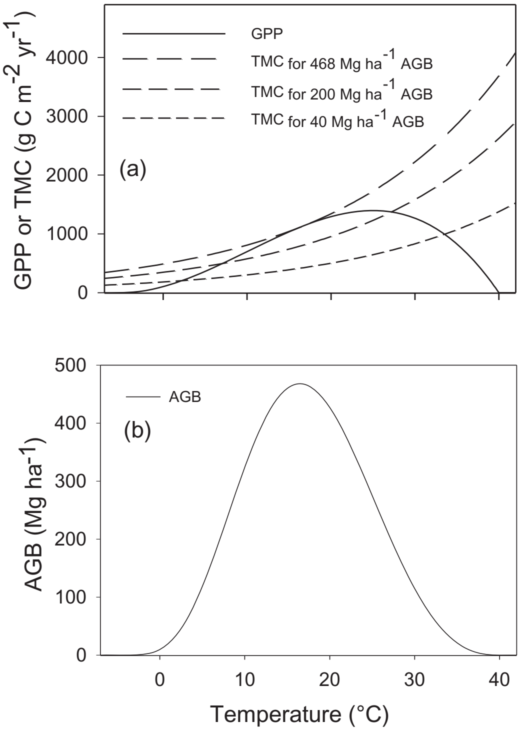

Figure 2 (a) The effects of temperature on gross primary productivity (GPP; solid line) and on total maintenance cost (TMC) for three different values of above-ground biomass (AGB; dashed lines), under the fitted models. (b) Predicted, old-growth forest above-ground biomass (AGB_{max}) as a function of temperature under the best-fit model. Values are calculated for a reference case in which temperature is seasonally and diurnally constant, the day is always 12 h long, and sun elevation is 60° at solar noon throughout the year.

Our model explained fully 50% of the variation in the old-growth AGB among 109 humid, lowland old-growth forests – none of which were included in the parameterization of the GPP and TMC models (Fig. 4). The RMSE for log-transformed AGB was 0.70, corresponding to approximately a two-fold deviation in untransformed AGB. The sensitivity analysis revealed that the proportion of the variance explained and the RMSE are robust to the specific parameter bounds and site selection criteria employed (see Appendix S2). Given our method of parameterization, r^2 and RMSE values are the appropriate measure of the success of our model. (In contrast, similarity in average values between predictions and observations is to be expected simply because the TMC function is parameterized based on measured AGB.)

DISCUSSION

Our models explained more than 50% of variation in GPP and TMC among the datasets to which they were fitted, and fully 50% of variation in old-growth biomass in an independent dataset. This strongly suggests that our approach successfully captured key influences of climate on energetic balances, and consequently old-growth biomass, in humid, lowland forests. Our model's underestimation of AGB for the highest AGB sites (Fig. 4) could in part be caused by biases towards higher AGB in the evaluation datasets, in particular oversampling of sites with higher AGB than average for their region ('majestic forest bias'; Phillips *et al.*, 2004) or oversampling in regions with higher AGB than average for their climates (e.g. more samples in the western coast of North America than of Europe). Another potential cause of underestimation is inclusion of younger forests in the datasets used for parameterizing the TMC model than in datasets used for evaluating predictions of old-growth forest biomass.

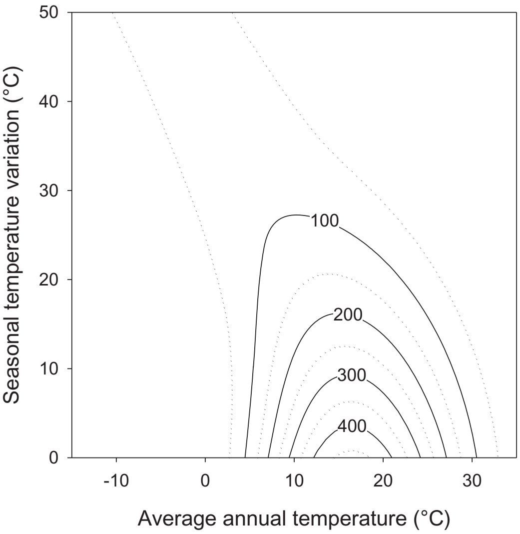

Figure 3 Predicted old-growth forest above-ground biomass (AGB_{max}; Mg ha^{-1}) in relation to average annual temperature and seasonal temperature variation, assuming a sinusoidal annual temperature cycle, no diurnal temperature variation, a 12-h day and sun elevation of 60° at solar noon. For this reference case, AGB_{max} achieves a peak value of 468 Mg ha^{-1} at a temperature of 16.5 °C with no temperature variation. Note that inclusion of diurnal temperature variation leads to a decrease in the average temperature at which AGB_{max} peaks, and an increase in that peak AGB_{max}. For example if days are 10 °C warmer than nights throughout the year, the highest AGB_{max} increases to 631 Mg ha^{-1} and occurs at an average temperature of 12.6 °C.

There have been few studies of AGB variation that span more than one continent. Stegen *et al.* (2011) analyzed 276 Gentry plots from the Americas and concluded that 'Climate generally explained little variation in forest biomass'. It is important to note that the small plot size in these studies increases sampling error, especially for high-biomass sites. Luyssaert *et al.* (2007) found weak patterns in a meta-analysis of over 100 plots; however, these sites included managed forests obviously increasing variation not explained by climate. Luyssaert *et al.* (2007) concluded that AGB does 'not follow a clear trend but overall higher biomass accumulation is observed in forests from the poles to the equator with the highest accumulation in temperate-humid evergreen forests. Within a climatic zone, forests in the humid biomes accumulate in general more

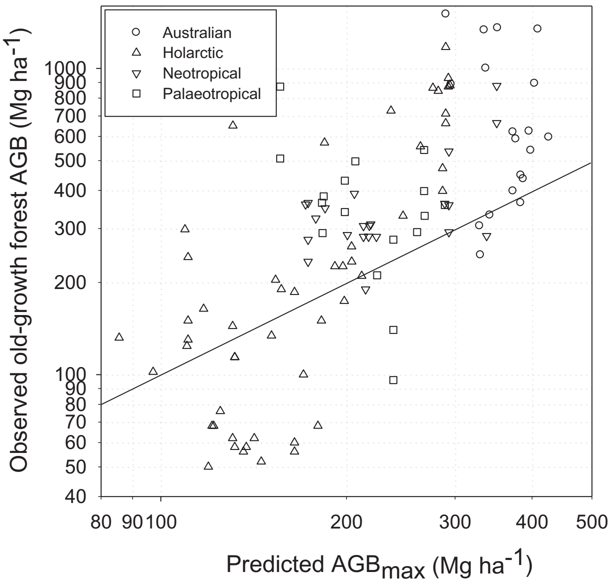

Figure 4 Measured above-ground biomass (AGB) in old-growth forests compared with predicted old-growth forest above-ground biomass (AGB$_{max}$) from the best-fit gross primary productivity (GPP) and total maintenance cost (TMC) models, relative to the 1:1 line (solid). The floristic kingdoms as in Corlett (2009).

biomass compared with forests in semiarid biomes'. Keith *et al.* (2009) evaluated another large dataset compiled from literature, and reported that 'temperate moist forests occurring where temperatures were cool and precipitation was moderately high had the highest biomass carbon stocks' but offered no explanation for why some temperate moist forests have low AGB. None of these studies evaluated relationships with seasonal temperature variation. It is possible that phenomenological models such as these could explain more geographic variation in AGB if they were restricted to old-growth forests and included seasonal temperature variation as a predictor. However, any such phenomenological models would still be of dubious utility for predicting forest biomass under novel future climates. In contrast, our more mechanistic model explained a large proportion (50%) of the global AGB variation among 109 humid lowland old-growth forest sites. And because it is mechanistic, our model provides more insight into underlying processes and a better basis for predicting forest biomass under novel future climates.

Our models lead to specific predictions for the impacts of global temperature change on forests. GPP is predicted to increase with increasing temperatures except in the lowland tropics (Fig. 2a), while MCB is predicted to increase with temperature everywhere. In combination, this leads AGB$_{max}$ to decrease with increasing temperature for a wide range of temperature regimes (Fig. 3). In the current climate of tropical lowland rain forests, an increase of approximately 4 °C is expected to halve AGB$_{max}$ in the long term (Fig. 3). A similar drastic change, but towards increasing AGB$_{max}$ with increasing temperature, is expected in cold and very maritime climates having little seasonal temperature variation (Fig. 3).

Clearly, there is more to explaining global variation in old-growth forest AGB than temperature and sun elevation alone, as is evident from the fact that neighbouring stands experiencing the same climate often have significantly different AGB. There are dozens of additional factors that influence GPP and/or MCB, and thus that would be expected to influence AGB$_{max}$, and could potentially be included in more complex models. The availability of water, soil nutrients and solar radiation to trees (influenced by clouds and other plants such as lianas) will clearly influence GPP of trees and thus AGB$_{max}$ and the number of trees per unit area influences MCB (Larjavaara, 2010). The life-history strategies of local woody plant species will also play a role, and are likely to interact with soils and climate as different strategies are favoured under different circumstances; these influences could potentially be captured in models that compete multiple functional types (Moorcroft *et al.*, 2001).

In the model presented here, we subsumed all components of maintenance – autotrophic respiration, leaf turnover, branch turnover, and tree turnover (mortality and recruitment) – into a single function, TMC, with a single dependence on temperature and biomass. This approach worked surprisingly well, as the fit of the resulting model was excellent with the exception of one unusual plot (Fig. 1b). Clearly, one obvious area for further model development is the separation of maintenance into components that can have distinct relationships to temperature and biomass, and parameterization of such models based on data for these components. Better models of TMC (and/or better models of GPP) would be expected to improve predictions of AGB$_{max}$, although it is important to note that more complex models are not necessarily better due to the increased danger of over-fitting (Burnham & Anderson, 1998).

A major challenge to ecology today is to predict the impact of global environmental change on old growth forest carbon stores and fluxes (Wright, 2005). Observations of current changes in AGB provide some insight (Phillips *et al.*, 1998; Myneni *et al.*, 2001; Chave, 2008; Lewis *et al.*, 2009), but do not enable us to forecast the final pool size for a given change in temperature. Complex dynamic global vegetation models (DGVMs) are in principle capable of estimating the final pool sizes, but global AGB variation is rarely reported (see Foley *et al.*, 1996, for an exception) possibly because it is difficult to model and regional testing has yielded unsatisfactory results (Delbart *et al.*, 2010). When DGVMs are applied to forecast the future, different models produce widely differing predictions, a pattern suggestive of overfitting that severely limits their utility for predictions under novel climates (Purves & Pacala, 2008). It seems unlikely that they could correctly predict future global patterns in AGB. Here, we presented a novel approach to understanding global AGB variation in humid lowland old-growth forests, an approach grounded in the dual influences of temperature on GPP and MCB. Our model explained half of current global AGB variation among humid lowland forests, and leads to concrete, testable predictions regarding the impacts of global temperature change. Future work that unites the best elements of these diverse approaches should contribute to a better understanding of climate impacts on forests today and in the future.

ACKNOWLEDGEMENTS

We thank Ryan A. Chisholm, Matteo Detto, David A. King, Pasi Kolari, Edbert G. Leigh and Jeremy W. Lichstein for helpful comments. We acknowledge the financial support of the HSBC Climate Partnership. We relied on data published in compiled articles and thank investigators and funding agencies of the original studies and various regional flux networks (Afriflux, AmeriFlux, AsiaFlux, CarboAfrica, CarboEurope-IP, ChinaFlux, Fluxnet-Canada, KoFlux, LBA, NECC, OzFlux, TCOS-Siberia, USCCC) and the Fluxnet project, whose support is essential for obtaining the measurements without which the type of integrated analyses conducted in this study would not be possible.

REFERENCES

Baldocchi, D. (2008) Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany*, **56**, 1–26.

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

Burnham, K. & Anderson, D. (1998) *Model selection and inference: a practical information-theoretic approach*. Springer, New York.

Byrd, R.H., Lu, P.H., Nocedal, J. & Zhu, C.Y. (1995) A limited memory algorithm for bound constrained optimization. *SIAM Journal on Scientific Computing*, **16**, 1190–1208.

Chave, J. (2008) Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biology*, **6**, 455–462.

Corlett, R. (2009) *The ecology of tropical east Asia*. Oxford University Press, Oxford.

Delbart, N., Ciais, P., Chave, J., Viovy, N., Malhi, Y. & Le Toan, T. (2010) Mortality as a key driver of the spatial distribution of aboveground biomass in Amazonian forest: results from a dynamic vegetation model. *Biogeosciences*, **7**, 3027–3039.

Development-Core-Team, R. (2008) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Fisher, J.B., Whittaker, R.J. & Malhi, Y. (2011) ET come home: potential evapotranspiration in geographical ecology. *Global Ecology and Biogeography*, **20**, 1–18.

Foley, J., Prentice, I., 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.

Forsythe, W.C., Rykiel, E.J., Stahl, R.S., Wu, H.I. & Schoolfield, R.M. (1995) A model comparison for daylength as a function of latitude and day of year. *Ecological Modelling*, **80**, 87–95.

Gale, J. (1972) Availability of carbon-dioxide for photosynthesis at high-altitudes – theoretical considerations. *Ecology*, **53**, 494–497.

Goulden, M.L., McMillan, A.M.S., Winston, G.C., Rocha, A.V., Manies, K.L., Harden, J.W. & Bond-Lamberty, B.P. (2011) Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Global Change Biology*, **17**, 855–871.

Gu, L.H., Baldocchi, D., Verma, S.B., Black, T.A., Vesala, T., Falge, E.M. & Dowty, P.R. (2002) Advantages of diffuse radiation for terrestrial ecosystem productivity. *Journal of Geophysical Research–Atmospheres*, **107**, 1–23.

Humphreys, E.R., Black, T.A., Morgenstern, K., Cai, T.B., Drewitt, G.B., Nesic, Z. & Trofymow, J.A. (2006) Carbon dioxide fluxes in coastal Douglas-fir stands at different stages of development after clearcut harvesting. *Agricultural and Forest Meteorology*, **140**, 6–22.

Jahan, N. & Gan, T.Y. (2009) Modeling gross primary production of deciduous forest using remotely sensed radiation and ecosystem variables. *Journal of Geophysical Research–Biogeosciences*, **114**, G04026.

Keeling, H.C. & Phillips, O.L. (2007) The global relationship between forest productivity and biomass. *Global Ecology and Biogeography*, **16**, 618–631.

Keith, H., Mackey, B.G. & Lindenmayer, D.B. (2009) Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences USA*, **106**, 11635–11640.

Kitayama, K. & Aiba, S.I. (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.

Kutsch, W.L., Eschenbach, C., Dilly, O., Middelhoff, U., Steinborn, W., Vanselow, R., Weisheit, K., Wotzel, J. & Kappen, L. (2001) The carbon cycle of contrasting landscape elements of the Bornhoved lake district. *Ecosystem approaches to landscape management in central Europe* (ed. by J.D. Tenhunen, R. Lenz and R. Hantschel), pp. 75–95. Springer-Verlag, Berlin.

Larjavaara, M. (2010) Maintenance cost, toppling risk and size of trees in a self-thinning stand. *Journal of Theoretical Biology*, **265**, 63–67.

Lefsky, M.A. (2010) A global forest canopy height map from the Moderate Resolution Imaging Spectroradiometer and the Geoscience Laser Altimeter System. *Geophysical Research Letters*, **37**, L15401.

Lenton, T.M. & Huntingford, C. (2003) Global terrestrial carbon storage and uncertainties in its temperature sensitivity examined with a simple model. *Global Change Biology*, **9**, 1333–1352.

Lewis, S.L., Lopez-Gonzalez, G., Sonké, B. *et al.* (2009) Increasing carbon storage in intact African tropical forests. *Nature*, **457**, 1003–1006.

Luyssaert, S., Inglima, I., Jung, M. *et al.* (2007) CO_2 balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, **13**, 2509–2537.

Mahecha, M.D., Reichstein, M., Carvalhais, N., Lasslop, G., Lange, H., Seneviratne, S.I., Vargas, R., Ammann, C., Arain, M.A., Cescatti, A., Janssens, I.A., Migliavacca, M., Montagnani, L. & Richardson, A.D. (2010) Global convergence in the temperature sensitivity of respiration at ecosystem level. *Science*, **329**, 838–840.

Mäkelä, A. & Valentine, H. (2001) The ratio of NPP to GPP: evidence of change over the course of stand development. *Tree Physiology*, **21**, 1015–1030.

Mäkelä, A., Pulkkinen, M., Kolari, P., Lagergren, F., Berbigier, P., Lindroth, A., Loustau, D., Nikinmaa, E., Vesala, T. & Hari, P. (2008) Developing an empirical model of stand GPP with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe. *Global Change Biology*, **14**, 92–108.

Malhi, Y., Wood, D., Baker, T.R. *et al.* (2006) The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology*, **12**, 1107–1138.

Moorcroft, P.R., Hurtt, G.C. & Pacala, S.W. (2001) A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecological Monographs*, **71**, 557–585.

Mori, S., Yamaji, K., Ishida, A. *et al.* (2010) Mixed-power scaling of whole-plant respiration from seedlings to giant trees. *Proceedings of the National Academy of Sciences USA*, **107**, 1447–1451.

Myneni, R.B., Dong, J., Tucker, C.J., Kaufmann, R.K., Kauppi, P.E., Liski, J., Zhou, L., Alexeyev, V. & Hughes, M.K. (2001) A large carbon sink in the woody biomass of northern forests. *Proceedings of the National Academy of Sciences USA*, **98**, 14784–14789.

New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface climate over global land areas. *Climate Research*, **21**, 1–25.

Pallardy, S. (2008) *Physiology of woody plants*. Academic Press, Burlington, VT.

Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Nunez, P.V., Vasquez, R.M., Laurance, S.G., Ferreira, L.V., Stern, M., Brown, S. & Grace, J. (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science*, **282**, 439–442.

Phillips, O.L., Baker, T.R., Arroyo, L. *et al.* (2004) Pattern and process in Amazon tree turnover, 1976-2001. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 381–407.

Purves, D. & Pacala, S. (2008) Predictive models of forest dynamics. *Science*, **320**, 1452–1453.

Raich, J.W., Russell, A.E., Kitayama, K., Parton, W.J. & Vitousek, P.M. (2006) Temperature influences carbon accumulation in moist tropical forests. *Ecology*, **87**, 76–87.

Rumney, G. (1968) *Climatology and world's climates*. Macmillan, Toronto, ON.

Ryan, M.G. (1991) Effects of climate change on plant respiration. *Ecological Applications*, **1**, 157–167.

Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P. & Senock, R.S. (2004) An experimental test of the causes of forest growth decline with stand age. *Ecological Monographs*, **74**, 393–414.

Sankaran, M., Hanan, N.P., Scholes, R.J. *et al.* (2005) Determinants of woody cover in African savannas. *Nature*, **438**, 846–849.

Slik, J.W.F., Aiba, S.-I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., Nagamasu, H., Nilus, R., Payne, J., Paoli, G., Poulsen, A.D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E. & Van Valkenburg, J.L.C.H. (2010) Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Global Ecology and Biogeography*, **19**, 50–60.

Spitters, C.J.T., Toussaint, H. & Goudriaan, J. (1986) Separating the diffuse and direct components of global radiation and its implications for modeling canopy photosynthesis. 1. Components of incoming radiation. *Agricultural and Forest Meteorology*, **38**, 217–229.

Stegen, J., Swenson, N., Enquist, B., White, E., Phillips, O., Jorgensen, P., Weiser, M., Mendoza, A.M. & Vargas, P.N. (2011) Variation in above-ground forest biomass across broad climatic gradients. *Global Ecology and Biogeography*, **20**, 744–754.

Thornthwaite, C. (1948) An approach toward a rational classification of climate. *Geographical Review*, **38**, 55–94.

Wright, S.J. (2005) Tropical forests in a changing environment. *Trends in Ecology and Evolution*, **20**, 553–560.

Zhang, Y., Xu, M., Chen, H. & Adams, J. (2009) Global pattern of NPP to GPP ratio derived from MODIS data: effects of ecosystem type, geographic location and climate. *Global Ecology and Biogeography*, **18**, 280–290.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data used in this study.
Appendix S2 Table of results of the sensitivity analysis.

BIOSKETCH

Markku Larjavaara was a post-doctoral fellow and **Helene C. Muller-Landau** is lead scientist of the CTFS/SI-GEO Global Forest Carbon Research Initiative (http://www.ctfs.si.edu/group/carbon). Markku's main research interest is the structure and size of trees.

Author contributions: M.L. developed the idea for the study, H.C.M. and M.L. did the analyses, and M.L. and H.C.M. wrote the paper.

Editor: José Paruelo