Biogeosciences Discuss., 10, 8611–8635, 2013
www.biogeosciences-discuss.net/10/8611/2013/
doi:10.5194/bgd-10-8611-2013

Biogeosciences
Discussions
Open Access

Predicting tree heights for biomass estimates in tropical forests

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Received: 28 March 2013 – Accepted: 2 May 2013 – Published: 23 May 2013

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

The recent development of REDD+ mechanisms require reliable estimation of carbon stocks, especially in tropical forests that are particularly threatened by global changes. Even if tree height is a crucial variable to compute the above-ground forest biomass, tree heights are rarely measured in large-scale forest census because it requires consequent extra-effort. Tree height have thus to be predicted thanks to height models.

Height and diameter of all trees above 10 cm of diameter were measured in thirty-three half-ha plots and nine one-ha plots throughout the northern French Guiana, an area with substantial climate and environmental gradients. We compared four different model shapes and found that the Michaelis–Menten shape was the most appropriate for the tree biomass prediction. Model parameters values were significantly different from one forest plot to another and neglecting these differences would lead to large errors in biomass estimates.

Variables from the forest stand structure explained a sufficient part of the plot-to-plot variations of the height model parameters to affect the AGB predictions. In the forest stands dominated by small trees, the trees were found to have rapid height growth for small diameters. In forest stands dominated by larger trees, the trees were found to have the greatest heights for large diameters. The above-ground biomass estimation uncertainty of the forest plots was reduced by the use of the forest structure-based height model. It demonstrates the feasibility and the importance of height modeling in tropical forest for carbon mapping.

Tree height is definitely an important variable for AGB estimations. When the tree heights are not measured in an inventory, they can be predicted with a height-diameter model. This model can account for plot-to plot variations in height-diameter relationship thank to variables describing the plots. The variables describing the stand structure of the plots are efficient for this. We found that variables describing the plot environment (rainfall, topography,. . .) do not improve the model much.

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1 Introduction

Tropical forests are an important and dynamic stock of carbon on earth: they account for 40 % of the carbon stored in the earth vegetation (Gibbs et al., 2007). Accurate estimates of Above-Ground Biomass (AGB) for tropical forests are needed to assess the spatial and temporal variation of these carbon stocks (Houghton et al., 2001). The AGB estimations have direct applications to forest management in the light of the recent developments of the carbon market and REDD+ (IPCC, 2000; Gibbs et al., 2007). Though considerable groundwork is being done, models used to predict biomass are often rough and need further improvements to lower biases and uncertainties (Houghton et al., 2001; Chave et al., 2005). Nowadays, AGB spatial extrapolation methods mostly rely on remote sensing data (Asner et al., 2010; Saatchi et al., 2011; Baccini et al., 2012). While very promising, these methods still require calibration points from well-known forest plot inventories (Lucas et al., 2002).

Forest census plots typically consist of various measurements of properties of all individual trees encountered on a given surface. Diameters at Breast Height (DBH) are always measured, generally starting at 10 cm. Depending on the inventory effort, additional information such as trees height or species identity may be recorded. The AGB of a forest plot is the sum of the AGB of the trees belonging to this plot.

Tree AGB models use biological variables describing a tree to predict its individual AGB (Brown et al., 1989; Brown, 1997; Araujo et al., 1999). The best models use the tree DBH, the tree height, and the tree wood density (Wood Specific Gravity, WSG) to catch the variability of tree biomass (Chave et al., 2005). Among these variables, the DBH is measured in the field and the effect of WSG is unclear for some authors (Molto et al., 2012).

Thus, for AGB prediction, tree height is a key variable that is generally not measured. It thus has to be predicted. In boreal forests, classical height models predict a tree height from its DBH for a given species (Sharma and Parton, 2007). However, the biodiversity of tropical regions prevents the use of height models that include a species effect. In the past, various Height–DBH model shapes have been proposed (Huang et al., 1992) but their applications to large scale tropical forests are rare (Brown et al., 1989; Feldpausch et al., 2011). The general objective of the paper is to explore the possibility to include additional information, such as structure and environmental variables, into the Height–DBH model in order to build a flexible model that can be used for AGB estimations in different landscape context.

We used a dataset from French Guiana, consisting of 42 forest plots. These plot inventories are suitable for AGB assessments (IPCC, 2000): DBH measured above 10 cm, height measures, species identification. The plots are situated in the northern part of French Guiana and were chosen to represent the contrasted landscape of the region (Ferry et al., 2010; Baraloto et al., 2011; Gond et al., 2011). More specifically, we asked the following questions:

1. Which Height–DBH model shape is both robust and convenient to use?

2. Do the Height–DBH model parameters vary between sites? If true, do these variations affect the AGB predictions?

3. Can the forest plot stand structures and forest local environment explain the variability of the Height–DBH model coefficients?

To reach the objective of setting a Height–DBH model for AGB predictions, height models are evaluated on their ability to replace measured heights in the forest plot for AGB predictions. We use a tree AGB model set in French Guiana. The AGB model uses tree height, tree DBH, and tree WSG to predict tree fresh AGB. It allow for uncertainty from height and WSG predictions propagation through a Monte-Carlo sampling process (Molto et al., 2012). To evaluate the performance of a Height–DBH model, we predict the AGBs of the trees using 1-measured heights and 2-predicted heights. The degradation of the precision of the AGB prediction between 1- and 2- gives us a measure of the performance of the Height–DBH model.

2 Material and methods

2.1 French Guiana

The study was conducted in French Guiana. The climate of the region is equatorial, with two main seasons: a dry season from August to mid-November and a rainy season (often interrupted by a short drier period in March) from December to April (Wagner et al., 2011). The relief comprises a hill system within a dense hydrographic network. Rainforests cover almost all the study area.

2.2 Forest plots

Inventory data came from two projects recently conducted in French Guiana. Description of the forest plots is available in the Supplement S2.

- Inventories from the AMALIN project (Baraloto et al., 2011): 33 plot spread in various landscapes and topographical contexts (ridges, plateau, and lowlands). DBHs and tree heights were measured by a team of trained experts. The plots are divided in 2 subplots (details in (Baraloto et al., 2011) and represent a 0.1 hectare area (trees with DBH ≥ 10 cm) nested in a 0.5 hectare area (trees with DBH ≥ 20 cm).
- Inventories from the BRIDGE project citepBaraloto2010a: 9 one-hectare plots where trees with DBH ≥ 10 were measured for DBHs and heights. Heights were measured with various methods, mainly lasers and ropes when climbers could approach the top of the trees. The different methods were compared on field and showed very consistent estimates.

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2.3 Forest plots descriptors

2.3.1 Descriptors of the forest structure

We chose variables commonly used by foresters to describe the stand DBH structure: the basal area (in m^2 per hectare) and the relative frequencies of four classes of stem size (between 10 cm and 20 cm, 20 cm and 40 cm, 40 cm and 60 cm, and above 60 cm). To avoid mathematical singularity, the proportion of stems between 20 and 40 cm was discarded from the data. These descriptors were computed from DBHs measurements only and thus are always available in standard forest inventories.

2.3.2 Descriptors of the environment

We chose to work with mainstream, widely available environmental variables. Four of these were computed from a Digital Terrain Model (DTM) with 90 m-sided squared cells (NASA SRTM missions). (i) The drained area measures the surface of the hydraulic basin that flows through a cell. A low value indicates cells located close to the limit of two basins, whereas the highest values indicate cells located downstream. (ii) The hydraulic altitude was computed from the 3rd order hydraulic system. The hydraulic altitude of a cell is its altitude above the closest stream of its hydraulic basin. Lowest values (including 0), indicate that the forest plot is located in a potentially temporarily flooded area while the highest values indicate that the forest plot is located at a top-hill area. (iii) The slope of each cell was computed with a 180 m lag (2 cells). (iv) The Terrain Ruggedness Index (TRI) was computed with a 20 cells lag (1800 m) to catch the difference between flat and more mountainous landscapes. Two environmental variables were computed from the NASA TRMM rainfall data. One was the annual average rainfall in the ten last years (in mm); the other was a dry season index (DSI), computed as the average number of months with a rainfall below 100 mm (Wagner et al., 2012). The dry season index quantifies the length of the annual hydraulic stress for trees. All maps and geographical information were computed with SAGA (Bock et al., 2004).

2.4 Height–DBH model shapes

M1 (Log-linear, Eq. 1): This Height–DBH model has already been used for Height–DBH modeling (Nogueira et al., 2008). Classically the error term was additive Normal, but we used a multiplicative Log-Normal to better address heteroscedasticity. The model may give negatives values for DBH lower than 1, but this is not a problem since the DBH are larger than 10 in standard forest inventories. The model has no horizontal asymptote for large values of DBH but thanks to the log function, the increase for large DBH values is extremely slow.

$$\begin{cases} H_i = (\alpha + \beta \times \log \mathrm{DBH}_i)\,\varepsilon_i \\ \varepsilon_i \sim \mathrm{LN}(0, \sigma^2) \end{cases} \tag{1}$$

M2 (Log-log, Eq. 2): This model is very frequently used in forest ecology (Brown et al., 1989; Feldpausch et al., 2011). However, the existence of factors limiting the tree growth in height but not in DBH may question its basic assumptions. Indeed, this model is known for over-shooting the height of the large trees (Feldpausch et al., 2011).

$$\begin{cases} H_i = \exp(\alpha + \beta \times \log \mathrm{DBH}_i)\,\varepsilon_i \\ \varepsilon_i \sim \mathrm{LN}(0, \sigma^2) \end{cases} \tag{2}$$

M3 (simplified Weibull, Eq. 3): This non-linear model is common in Height–DBH relationship modeling (Fang and Bailey, 1998; Feldpausch et al., 2011). Its shape presents an oblique asymptote with slope α/β at $(0,0)$ and a horizontal asymptote $H = \alpha$ when DBH is large.

$$\begin{cases} H_i = \alpha\left(1 - \exp\left(-\mathrm{DBH}_i/\beta\right)\right)\varepsilon_i \\ \varepsilon_i \sim \mathrm{LN}(0, \sigma^2) \end{cases} \tag{3}$$

M4 (Michaelis–Menten, Eq. 4): This non-linear model, while very common in chemistry, has rarely been employed to model Height–DBH relationships (Huang et al., 1992).

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However, it presents all the required features: positive, increasing, with an oblique tangent line with slope $\beta = \alpha/\gamma$ in (0,0) and a horizontal asymptote $H = \alpha$ when DBH is large.

$$\begin{cases} H_i = \frac{\alpha \times \mathrm{DBH}_i}{\gamma + \mathrm{DBH}_i} \varepsilon_i \\ \varepsilon_i \sim \mathrm{LN}(0, \sigma^2) \end{cases} \tag{4}$$

The model was re-arranged as follow to ease the parameter inference:

$$\begin{cases} H_i = \frac{1}{1/\alpha + \beta/\mathrm{DBH}_i} \varepsilon_i \\ \varepsilon_i \sim \mathrm{LN}(0, \sigma^2) \end{cases} \tag{5}$$

All models have 3 parameters: 2 for the shape and 1 for the variance of the error term. In order to mechanistically increase the model uncertainty with height and DBH, the error term was modeled by a Log-Normal distribution. Keeping in mind our objective is biomass prediction, each Height–DBH observation was weighted by a proxy w_i of the biomass of each single tree 5.

$$w_i = \mathrm{DBH}_i^2 \times H_i \tag{6}$$

The weights w_i were normalized in each plot to sum to the number of observations.

The models M1 to M4 were calibrated in each forest plot. Parameter estimations were conducted using MCMC methods (see Supplement S1). After discarding a burn-in sample and a thinning of the chains, 1000 samples of the posterior distribution of each parameter is kept (for M4, the posterior distribution of the parameters are presented on Fig. 1). The models inferred independently in each forest plot are referred to as the "site-specific" Height–DBH model.

2.5 Height–DBH model shape selection

For each forest plot, the AGB of the plot was computed. The AGB of a forest plot is the sum of the AGB of the trees from this plot divided by the surface of the plot,

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in $\mathrm{Mg\,ha^{-1}}$. The tree AGB model predicts the mass of a tree from its DBH, height, and WSG 7. Uncertainties from height predictions, WSG predictions, and tree AGB model parameters are propagated through Monte-Carlo samples of their respective distributions (Molto et al., 2012).

$$\begin{cases} \log \mathrm{AGB}_i = \beta_0 + \beta_1 \log \mathrm{DBH}_i + \beta_2 \log H_i + \beta_3 \log \mathrm{WSG}_i + \varepsilon_i \\ \varepsilon_i \sim N(0, \sigma^2) \end{cases} \quad (7)$$

In each forest plot, AGB was predicted 1- using field-measured heights, 2- with predicted heights. When the AGB of a tree was predicted (Eq. 7) with a height H_i predicted from one of the four height models, Monte-Carlo samples of the predicted height H_i are generated from the posterior samples of the parameters and error term of the Height–DBH model.

The forest plots AGB distributions obtained from each height predictions were compared with the AGB distribution obtained from measured height using the RMSE (Root mean squared error) (Fig. 2). The selected Height–DBH model was thereafter noted M*. In addition, the selected model M* was calibrated on the entire dataset without site effect. This model is called "regional" model.

2.6 Environment and forest structure effect on the height model parameters

2.6.1 Model definition

A new model was built where the shape parameters α and β in the selected model M* was replaced by a log-linear combination of the variables x_j describing the forest plots p (Eq. 7). The parameter σ was now unique and we did not try to explain its plot-to-plot variation for identifiability reasons. The variables x_j were scaled so the coefficients of the log-linear combination can be compared to each other.

We used the exponential function to constrain the values of the parameters α_p and β_p to be positive. In the models M2, M3, and M4, the coefficients α and β are positive for physical reasons: the height is a positive value and the height increases with the DBH. In the model M1, the α parameter is not necessarily positive. The observations were weighted as previously (Eq. 6). For algorithm details of the estimation of θ_α, I_α, θ_β, and I_β, see Supplement S1.

$$\begin{cases} \alpha_p = \exp\left(\theta_{\alpha,0} + \sum_j \theta_{\alpha,j}\theta_{\alpha,j}x_{j,p}\right) \\ \beta_p = \exp\left(\theta_{\beta,0} + \sum_j \theta_{\beta,j}\theta_{\beta,j}x_{j,p}\right) \end{cases} \quad (8)$$

We used the method set by (Kuo and Mallick, 1998) to select the variables x_j to be integrated in the final model. During parameter inference (see Supplement S1), an indicator $i_\alpha j$ (respectively $i_\beta j$) associated with each variable x_j for the parameter α (respectively β) can take two values: 1 indicates that the variable is kept in the model, 0 indicates that the variable is not kept in the model (Eq. 7). Thanks to the indicators, the MCMC algorithm explores different combinations of variables.

To decide whether a variable x_j is kept in the model or not, we compute its percentage of presence in the explored models. This percentage is computed as the mean of the MCMC chain values of the indicator $i_{\alpha,j}$ (respectively $i_{\beta,j}$) after a burn-in removal and a thinning.

Usually, this percentage had the shape of a plateau followed by a rapid decrease. We aimed to keep the variables with a percent of selection close to the value of the plateau. The selected variables implicated in the replacement of α and β are not necessarily the same (Fig. 3).

2.6.2 Variable selection

Because the environment has an obvious effect on the forest structure, we could not consider the structure and environmental variables in a single step. Thus, we first replaced the α and β coefficients by a linear combination of the stand structure variables

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only. The structure variables were selected with the method described above. The resulting model is called "stand structure model" (Fig. 3, panels 1 and 3). Then, the environment variables were added to the previous stand structure model. The variable selection procedure was run again, selecting the environment variables only. In other words, an environmental variable was selected only if it caught residual variance that was not caught by the formerly-selected structure variables (Fig. 3, panels 2 and 4).

As for the comparison of the model shapes, the heights predicted with the stand structure model and the environment model were used to compute the AGB of the plots. In its ability to predict height to predict AGB, the best model including structure and eventually environmental variables is a compromise between the regional model (worst case) and the site-specific model (best case). The comparison of the AGB prediction RMSE allows quantifying how the variables describing the forest plots improve the regional model and how far the performances are from the site-specific model.

3 Results

3.1 Model shape selection

Overall, we found that α and β coefficients were different from one site to another (Fig. 1 for M4 model), showing that the Height–DBH relationship varies between locations. The posterior distributions of both parameters α and β were somewhat correlated ($r = -0.81$), suggesting that the forest properties they catch are not independent. Using the α, β, and σ coefficients of the site-specific M* model, the heights were predicted with each model in each forest plot for a tree of 50 cm DBH (Fig. 1).

RMSEs being quite similar and completely overlapping (Fig. 2), we chose to focus on model M4 for two main reasons: 1 – it has biological-meaningful coefficients (contrary to M1 and M2); 2 – it is easier to manipulate than M3 and its exponential function.

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3.2 Environment and structure variable selection

The selected structure variables explaining the observed variation of α are the basal area (negative effect), the proportion of small stems (strong negative effect), and the proportion of medium stems (negative effect). In addition, the slope (positive effect) and the rainfall (negative effect) were selected among the environment variables (Fig. 3, Table 1). The selected structure variables involved in the replacement of β are the proportion of small stems (strong positive effect) and the proportion of bigger stems (positive effect). The rainfall (positive effect) and the drained area (negative effect) were selected among the environment variables (Fig. 3, Table 1) to complete the structure variables. The variables selected for the replacement of α and β are not shared. All the found parameters exclude zero from their 95 % confidence interval. The highest values were obtained for the proportion of small stems, highlighting its great explicative power. Environmental variables have very weak effects.

3.3 AGB prediction

The RMSE of the model including structure and/or environment variables was larger than the RMSE of the site-specific model and smaller than the RMSE of the universal model (Fig. 4). The RMSE of the model including environment variables did not differ from the RMSE of the model using structure variables only (Fig. 4).

4 Discussion

Using a dataset from diverse neotropical forests from French Guiana, we modeled the Height–DBH relation using the Michaelis–Menten equation. The Height–DBH relation was varying between locations, affecting the AGB estimations. We then demonstrated that part of the Height–DBH relation variability can be explained by variables issued from the forest structure and, less, from descriptors of the local environment.

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4.1 Model choice and parameter values in the site-specific model

On their performances to predict height to predict AGB, the 4 models were very close each other. We believed that our peculiar weighting was responsible for this tightness, because it gave a high weight to the trees with a high biomass. This suggested that, with these weights, one can use any of these four models to predict heights to predict biomass. However, the replacement of the parameters by combinations of environment variables may be different. We also emphasize that the Michaelis–Menten model mathematical form is the easiest to handle (no exponential function). Though the exponential model has been used in the past (Feldpausch et al., 2012) found that the Weibull model was the most appropriate for biomass prediction (they did not consider the Michaelis–Menten model). We thus conclude that asymptotic models should be preferred to other shapes.

The α and β model parameters differed largely between forest plots (Fig. 1). This demonstrates that the Height–DBH relationship was not the same in each plot, leading to contrasting Height–DBH relationships and contrasting AGB values.

The α parameters represented the value of the horizontal asymptote for the largest DBH. This value was highly correlated with the maximum observed height in each forest plot ($\alpha = 1.06 \times H_{max}$, $R^2 = 0.98$, RSE = 6.7).

This result has important practical consequences. If it is not reasonable to measure the height of all trees in large-scale inventories, but it is feasible to measure the 10 higher trees or so to get the maximum height of a forest plot. Moreover, the maximum height of a forest plot is a direct output from LiDAR measurements. In either of these cases, the α parameter wont be predicted from environmental variables but will be estimated more or less directly. Knowing the α parameter, the construction of the Height–DBH model is more simple, straightforward, and precise because it depends only on finding β.

The β parameter represented the slope of the oblique tangent in (0, 0). The larger β is, the faster the trees reach the asymptote. β values showed less variation than

α between forest plots (Fig. 1). This suggests that the parameter could be inferred at the region level, with no site effect on its value. However, because some plot to plot differences remained, we decided to test the forest structure and environment effect on this parameter. If one aims to build a Height–DBH model estimating α as suggested above, one could consider using a constant β parameter for simplicity.

4.2 Structure variables

The competition for light between trees has been identified as a major driver of the trees height trajectory. Some authors suggest that the Basal area is a better expression of the competition than the stem density (Hummel, 2000; King et al., 2009). However, we found a weak and negative effect of BA on α and it was not kept for β explanation.

In our case-study, we believe that the Height–DBH relationship variation is better explained by the forest succession. After perturbation, plants compete for resources. The younger stands contain a high proportion of small trees, while self-thinning rules cause the older stands to contain a relatively small number of large trees (Clark, 1996; Guariguata and Ostertag, 2001; Luyssaert et al., 2008). Indeed, the proportion of small trees (10–20 cm DBH) has a strong positive effect on β together with a strong negative effect on α. In a young forest patch with high density of small trees, the tree competition cause trees to grow faster in height (Hummel, 2000), but the relative youth of the forest patch may also cause the forest stand to have lower maximum heights (effect on α). The small positive effect of the proportion of biggest trees (more than 60 cm DBH) on β also suggests that the presence of a large tree, limiting the light resource, also cause the small trees to grow faster in height.

4.3 Environment variables

Because the environment has an obvious effect on the forest structure (Baraloto et al., 2011), we decoupled in time the inclusion of structure and environment variables in the final model. The negative effect of the rainfall on α is clearly unexpected. The rainfall, related to the water availability, has largely been described as a positive driver of the forest height (Koch et al., 2004; Ryan et al., 2006). The negative effect of the drained area on β indicates that the trees grow slower in height in a seasonally flooded or waterlogged terrain. This is explained by (i) a greater light availability (Ferry et al., 2010) in turn linked to higher turnover rates (Madelaine et al., 2007; Ferry et al., 2010) and (ii) higher mechanical constraints due to the lower soil stability in flooded areas (Gale and Barfod, 1999; Gale and Hall, 2001). The trade-offs between variables in α and β replacements, between α and β replacements, and the low values of the model parameters makes that we should consider the highlighted patterns carefully.

4.4 Perspectives

In this study we showed that part of the variability of the Height–DBH relationship was mainly explained by the maturity of the stand, expressed as the proportion of small trees (10–20 cm DBH). While Basal Area and rainfall were the most important variables at world scale (Feldpausch et al., 2011), we did not find them crucial at the regional scale in French Guiana. Our study did not include any soil effect on the Height–DBH relationship, though we interpreted the effect of high drained areas as a possible indicator of soil instability. If available, information on the soil properties has been proved to be meaningful when studying the trees heights (Aiba and Kitayama, 1999; Quesada et al., 2009; Feldpausch et al., 2011).

To go even further, more sophisticated model could be inferred incorporating much more information at the tree level. For example, if the botanical information is available, a trait-based model may provide substantial improvement. The functional traits have proven to catch information on species biological properties that may be related to the Height–DBH relationship (Baraloto et al., 2010; Hérault et al., 2011).

Now the model can be used to predict the coefficients of a Height–DBH model on the whole region of French Guiana. The new AGB estimates using the new predicted height will help us to understand the spatial patterns of AGB variations and produce more accurate Carbon stock estimates.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/10/8611/2013/ bgd-10-8611-2013-supplement.pdf.

Acknowledgements. This study is part of the GUYASIM project (31032, programme operationnel FEDER 2007–2013), with financial support provided by European structural funds. This work has benefited from an "Investissement d'Avenir" grant managed by Agence Nationale de la Recherche (CEBA, ref. ANR-10-LABX-0025).

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Table 1. Median and 95 % Confidence Interval (CI) of the effects of structure variables and environment variables on coefficients α and β of the model M4 (Eq. (5), Eq. (7), Fig. 3).

Variable j	$\theta_{\alpha,j}$ Median and 95 % CI	$\theta_{\beta,j}$ Median and 95 % CI
Intercept	3.785[3.755, 3.802]	0.595[0.553, 0.634]
Basal area	−0.017[−0.027, −0.008]	
Prop_10–20	−0.135[−0.146, −0.12]	0.11[0.098, 0.136]
Prop_40–60	−0.023[−0.036, −0.004]	
Prop_60+		0.044[0.032, 0.055]
slope	0.025[0.015, 0.036]	
rainfall	−0.028[−0.048, −0.008]	0.051[0.023, 0.081]
log_area_drain		−0.04[−0.048, −0.033]

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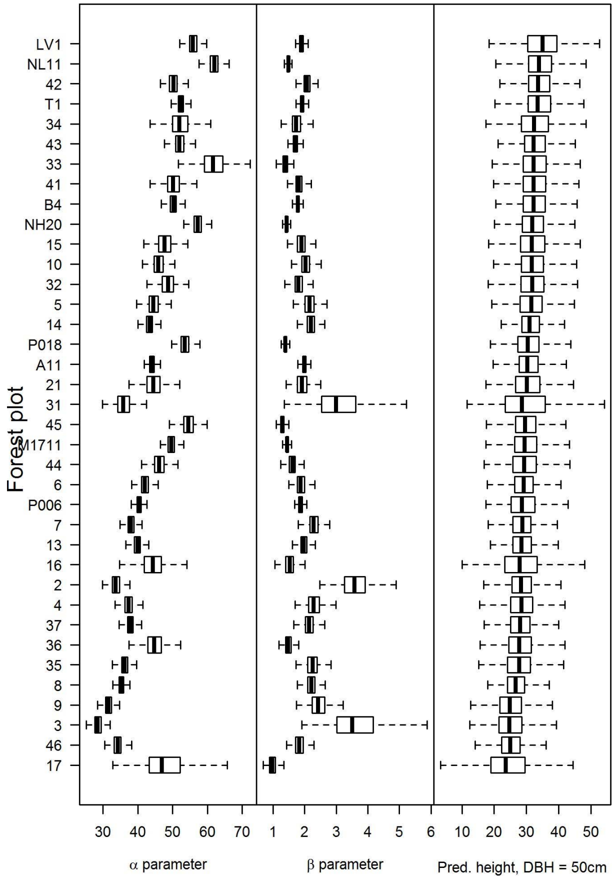

Fig. 1. Posterior distribution of the α, β, and σ coefficients of the M4 model: $H_i = 1/(1/\beta + \alpha/\mathrm{DBH}_i)\varepsilon_i$, $\varepsilon_i \sim \mathrm{LN}(0,\sigma^2)$. The last panel presents the predicted height distribution of a tree with a DBH of 50 cm.

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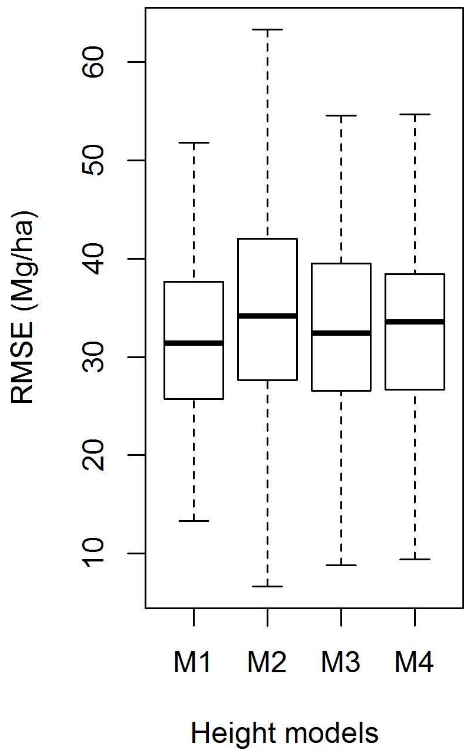

Fig. 2. Boxplots of the mean RMSE of the AGB predictions in the 42 forest plots with tree heights predicted by four different models: log-linear (M1), log-log (M2), Weibull (M3), and Michaelis–Menten (M4).

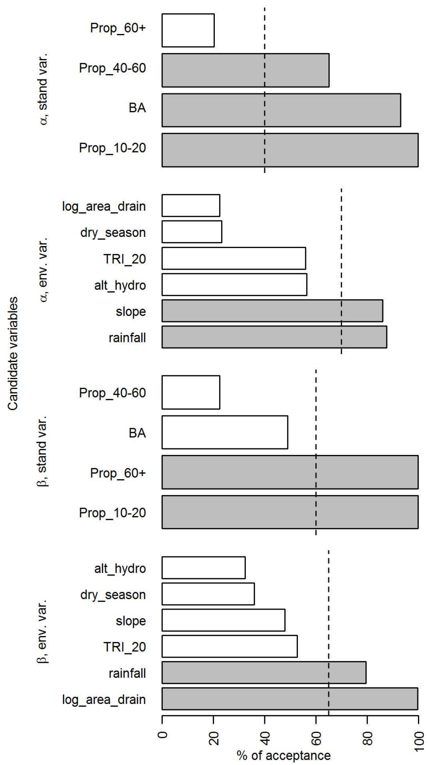

Fig. 3. Variable selection. The bars represent the % of presence of the variables in the model, computed from the posterior values of the indicators $i_{\alpha,j}$ and $i_{\beta,j}$ (Eq. 8). The dotted lines indicate, in each selection process, which cut-off limit is chosen for the acceptance of a variable in the definitive models. Prop_X_Y = proportion of stems between and Y cm, BA = Basal Area, TRI_20 = Terrain Ruggedness Index. The grey bar indicates the variables kept in the definitive model. The structure variables (first and third panels) were selected first. Then, keeping the selected structure variables, environmental variables were added to improve the model (second and last panels).

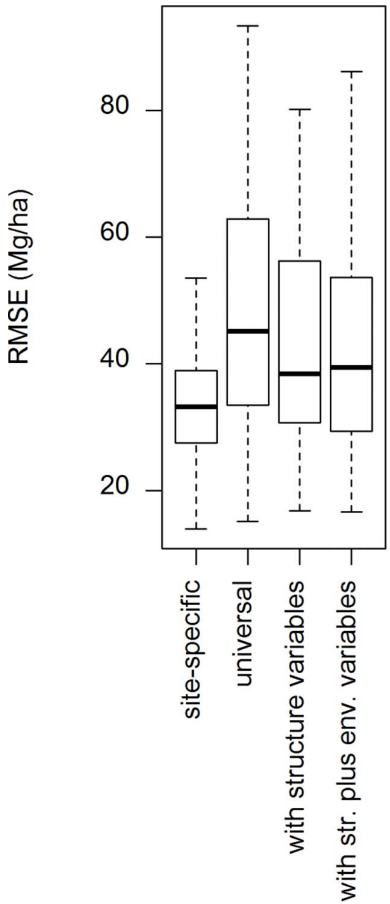

Fig. 4. Boxplots of the mean RMSE of the AGB predictions in the 42 forest plots with tree heights predicted by four different Height–DBH models: site-specific, universal, based on structure variables only, and based on structure variables completed with environment variables.

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