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Teak growth, yield- and thinnings' simulation in volume and biomass in Colombia

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Abstract. In the Colombian Caribbean, 44 permanent sampling plots (PSPs) on teak (*Tectona grandis*) plantations in 20 stands ranging in age from 3 to 20 years have been measured annually for 17 years. We have developed a compatible growth and yield model using the state-space approach and Kopf's growth equation fitted by nonlinear mixed-effects-models (NLMEMs). For each site index class, the transition function of the basal area depends on the initial basal area (G_1) and the initial age (t_1), projected to a future basal area (G_2) and its age (t_2). In the transition function, the previous thinnings were added to not underestimate the total yield. We use NLMEMs to prevent autocorrelation by modeling annual measurements in the PSPs. The transition function is inserted in allometric stand models of three key variables: volume over bark, the volume under bark, and above-ground biomass. Tree allometric models for volume over bark, the volume under bark, and biomass were parameterized, self-validated, independently validated, and recalibrated. Stand allometric models for the same three key variables, as a function of the stand basal area, were parameterized by using NLMEMs to evaluate proportional variance to the mean and variance as a potential function of the mean. In both tree and stand allometric models, the assumptions of the regression have been fulfilled. The resulting growth and yield model allows for the estimation of current growth and predicts future yields in volumes and above-ground biomass arising from thinnings treatments. The proposed model is a useful tool for teak efficient plantations management. The proposed growth models for teak in this paper may have a potential utility in newly teak planted areas, where such tools are scarce or non-existent.
Keywords: allometric models, compatible growth and yield models, independent validation, state-space approach, *Tectona grandis*

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Introduction

Perhaps the state-space approach (SSA) is the most advanced technique available today to generate compatible growth and yield models in forest plantations. The SSA relies on the assumption that the state of a system at any given time contains the cumulated information of the past, and only information on the present is needed to predict the future behavior of the system (García 1994, Nord-Larsen & Johannsen 2007, Weiskittel et al. 2011). Only recently, this technique has been incorporated to study the growth of teak in India (Tewari et al. 2014, Tewari & Singh 2018), under a very different monsoon climate from those of the Neotropics, and in Venezuela (Quintero et al. 2012, Jerez et al. 2015). Only in the studies from Venezuela, the thinnings were simulated.

Teak (*Tectona grandis* L. f.) is the most valuable tropical timber species under cultivation (Ladrach 2009, Kollert & Kleine 2017). Although teak has been planted in the Neotropics since 1913 (Ladrach 2009), and since 1884 in Africa (Wadsworth 1997), studies of its growth and yield have limitations to be applied in some sites and management conditions where this species currently is cultivated. Some of these limitations are explained in the next three paragraphs.

Most published equations to estimate the volume or biomass of teak trees use the diameter at breast height (*dbh*) and the height (*Ht*) of the trees, either as independent variables, or combined into a single expression. The decision on the selection of the most appropriate model is generally based only on the quality of the statistical adjustment. However, since *dbh* and *Ht* are positively correlated because they are allometically related ($Ht = \alpha(dbh)^{\beta}$), it must be verified whether these two variables or the combined variable, have autocorrelation using an appropriate test that is not usually done. Frequently, non-linear volume and biomass equations are transformed logarithmically. This procedure tends to increase statistical adjustment and avoid heteroskedasticity. However, it has a cost represented in a systematic bias that reduces the volume or biomass of trees when the equations become non-linear again. This bias was initially described by Meyer (1941), who proposed a remedial measure. Subsequently, Satoo (1982) reviewed all proposals to avoid this bias, although they are often not used in teak. This bias has dramatic effects when calculating the volume or biomass per hectare. Zapata et al. (2003) found, by using three different proposals to avoid the bias in biomass equations, that it was underestimated by 23 to 24%, although the logarithmic equation reached an R^2 of 97.9%.

When using the SSA, the differential equations of the form $dy/dt = f(y)$ are integrated to obtain $y = f(t)$ equations usually fitted by least square methods, where y can be expressed in volume, biomass, or basal area per hectare, among other variables, and t is the time (years). If the variable y comes from permanent sampling plots (PSPs) in which censuses are repeated over time, the resulting equations are affected by autocorrelation violating a regression assumption. Not all studies using the SSA on teak have filtered the autocorrelation. In whole-stands growth models, as is the case in all revised teak studies, when there have been thinnings in the PSPs at an age t, the value of y thinned must be added in the following period to the standing y, to not underestimating the total yield. We have noted that this procedure has not been followed when using the SSA in teak based on thinned PSPs. The same problem arises when temporary sampling plots that have received thinning are used because, although the number of initially planted trees and the final number of trees can be known, their contribution to thinning in volume, basal area, and biomass is unknown.

Today, worldwide, forest plantations are used both to produce wood and to capture CO_2. Tropical forest plantations are very promising because of their rapid growth, allowing us to cost-effectively combining wood and CO_2 capture through biomass. Therefore, it is currently very important that the yield and growth models and thinnings simulation, express the yield both in volume as in biomass. Owing to the high monetary value of teak wood and the increase in planted area, it is necessary a more precise and site-specific knowledge on teak growth and yield. Up to now, it seems that no previous research in teak has included, in the same paper, yield models for the volume over and under bark, the biomass, and thinnings simulations of these three key variables.

The objectives of this study are: (i) to develop tree and stand allometric equations of volume (over bark and under bark) and above-ground biomass for teak and (ii) to develop simulation models of thinnings yield and final yield as a function of age, and site index, for volume with and without bark and for above-ground biomass. The models obtained should contribute to the efficient management of teak plantations, harvest planning, and the development of CO_2 capture projects in areas where this information is scarce or non-existent.

Methods

Study area

The study area is near the Caribbean coast of Colombia (Figure 1). The altitude varies between 60 and 110 m. The mean annual rainfall is 2,480 mm, with a unimodal annual-pattern of monthly rainfalls, peaking during June and July. January and February are dry months with rainfalls lower than potential evapotranspiration; the other months are wet. The mean annual temperature is 27 °C.

Data collection from PSPs

Twenty permanent sampling plots (PSPs) were established three years after planting. The number of PSPs increased during the following five years until completing 44. Of the total number of PSPs, 23 are 600 m^2 (30 m × 20 m), and the remaining 21 are 1000 m^2 (40 m × 25 m). The age of the PSPs ranged from 3 to 22 years old; they were established in 20 stands and two plantation areas (Figure 1). The PSPs

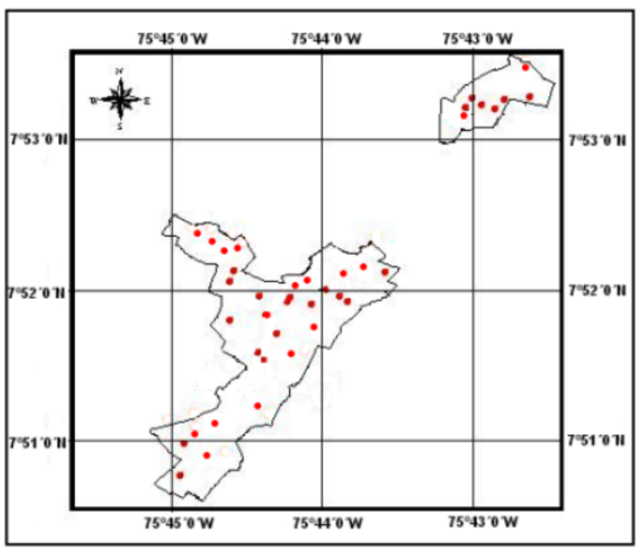


Figure 1
Study area showing the two planted areas in the Colombian Caribbean. The dots represent the permanent sampling plots (PSP).

were established in pure, even-aged stands and subjected to different management treatments, as follow: the initial planting from 1000 to 2500 trees · ha^{-1}, two or three manual weedings during the first 2 years, two prunings during the fifth year (up to 3 m stem height, leaving about 7–15 m of the top of the trees unpruned, depending on site quality), and during the ninth year (up to 6 m stem height, leaving about 4–18 m of the top of the trees unpruned, depending on site quality), and manual cleanings once a year from year 3 until clear-cutting. Thinnings were carried out during ages 7–8 and 12–13 to maintain approximately 26 $m^2 \cdot ha^{-1}$. Each year, during 17 years, the diameter at breast height (*dbh*) and the mean height of the dominant trees ($\overline{H}d$) was measured on each PSP. Six dominant trees per 600 m^2 plot and ten trees per 1000 m^2 plot were measured. Also, in each census and each PSP, the total height (*Ht*) of 20 trees, in the 600 m^2 PSPs, or 30 trees, in the 1000 m^2 PSPs of randomly selected trees, different from the dominant trees, was measured.

Site quality

The site index (*SI*) was determined on each plot, as the mean height of the 100 dominant trees per hectare ($\overline{H}d$) at a reference age of 12 (total age since planting), using eq. 1 (Torres et al. 2012):

$$SI = \overline{H}d\left[exp1.96\left(\frac{1}{t^{0.65}} - \frac{1}{12^{0.65}}\right)\right] \tag{1}$$

where *exp* is the base of the Naperian logarithms *e*, and *t* is the age in years.

Volume and above-ground biomass equations for individual trees

Allometric models were used to fit the volume (gross useful volume) over bark (*vob*) and under bark (*vub*) and the above-ground biomass (*b*) of individual trees as a function of *dbh*. Stands were categorized into 17-age classes ranging from 3 to 22 years. Within each age class (but outside each PSP) 6 trees were randomly selected, for a total of 102 trees that comprise the entire range of diameters for each PSP. Then, the *dbh* was measured on each tree with a diameter tape. Trees were felled with a chainsaw as close to the ground as possible. The *Ht* and useful lengths (H_c), which exclude the apical branches, were measured. The useful length of each stem (the distance from the stump to the point where the tree has thicker branches than the main trunk), was split into ten equal-length logs. The ends and middle diameters were measured on each log. From each of these three points, a piece of bark was removed and measured with a digital caliper. Logs were weighed in the field on an electronic balance (maximum weight of 150 ± 0.01 kg). At both ends of each log, approximately 5 cm thick cross-sections disks were cut and weighed in the field using an electronic balance (maximum weight of 1200 ± 0.5 g). The cross-sections disks were dried to a constant weight in a forced-air oven at 103 °C. Leaves, flowers, and fruits were removed from the branches. The primary branches, extending laterally from the main trunk, were separated from the thin secondary branches, and both groups were weighed. An approximately 1 kg representative sample was weighed from each group of branches and dried to constant weight at 103 °C.

Following the measurement of the diameter, the equivalent area was estimated for each section. To a cross-sectional disk cut from the base of the still-fresh trunk, its perimeter was reproduced on cardboard. On the cardboard, the cross-sectional area was measured with a digital planimeter, and the equivalent diameter estimated. Newton's formula for estimating the volume of each of the ten logs was used. By adding these ten logs, the volume of each stem results. The thickness of the bark was subtracted from each diameter to estimate the *vub*. The volume of each log was then measured, as previously described.

From the green weight (*Gw*) and dry weight (*Dw*) data, the ratio $r = Gw/Dw$ was calculated for each subsample (r_1 and r_2). Then were calculated $r_1 = Gw_1/Dw_1$, and $r_2 = Gw_2/Dw_2$, where Gw_1 and Gw_2 are the green weights of cross-sectional disk 1 and 2, respectively and Dw_1 and Dw_2 are the dry weight of cross-sectional disks 1and 2, respectively. The weighted average (*rw*) was calculated from the two sections of the ends of each log based on the dry weight contribution: $rw = [(Dw_1)(r_1) + (Dw_2)(r_2)]/(Dw_1 + Dw_2) = (Gw_1 + Gw_2)/(Dw_1 + Dw_2)$. When the diameter of a branch at point of attachment to the trunk was less than 10 cm, the dry weights of the thick branches were obtained by multiplying their green weight by the *rw* of the top section of the stem. When the diameter was greater than 10 cm, it was estimated as the main stem; splitting it into logs, and 5 cm cross-sectional taken from the ends. For the secondary branches, the dry weight was calculated by multiplying the green weight by the *rw* ratio from the subsample of thin branches. The total above-ground biomass of each tree (*b*) was therefore obtained by combining the dry weight of both the logs and branches.

One tree was randomly removed per every one year age classes (from age 3 to age 22), for a total of 17 trees. These trees were used for the validation of the allometric models. With the remaining 85 trees, allometric models (2) to (4) were fitted by nonlinear least squares (NLLS).

$$vob = \alpha_1(dbh)^{\beta_1} \tag{2}$$

$$vub = \alpha_2(dbh)^{\beta_2} \tag{3}$$

$$b = \alpha_3(dbh)^{\beta_3} \tag{4}$$

where *vob* and *vub* are in cubic meters per tree, *b* in kilograms per tree, α_i and β_i are unknown parameters to be estimated, and *dbh* is in centimeters. For models recalibration, we proceed as follows: if there were higher values on the criteria for independent validation of the 17-trees than in the self-validation of the best-weighted regressions using 85 trees, the allometric models were assessed using different weights. If, however, the predictions proved to be reliable, new models were estimated using all the data (102 trees). The goodness of fit was evaluated with the determination coefficient (R^2), the homogeneity of the errors' variance was examined with the modified Breusch–Pagan test (*B-P* test), normality of the residuals with the Shapiro-Wilk test (*S-W* test), and autocorrelation with the Durban-Watson test (*D-W* test) (Greene 2018). If regressions did not meet all regression assumptions, a new estimate was made with nonlinear weighted least squares (NLWLS) using four weights. The first two weights were based on the residuals obtained by the NLLS: the inverse of the residuals absolute value and the inverse of the residuals squared. The other two were: the inverse of the independent variable (*dbh*) and the inverse of the independent variable squared. The resulting 12 models (four for each variable: *vob*, *vub*, and *b*) were assessed by the same tests (R^2, *S-W* test, *B-P* test, and *D-W* test) before selecting a single model for each volume and above-ground biomass. Then, using data from the 17 previously selected trees to estimate the model, an independent validation was performed by residual plots and the following tests according to Vanclay (1994): the mean absolute difference, mean relative difference and model efficiency, where *y* is *vob*, *vub*, and *b* (eqs. 2 to 4), respectively.

Comparison with other models

To compare the resulting models, other regressions were fitted on ordinary least squares for *vob* and *vub* as a function of the combined variable dbh^2Ht, that has produced the best fit in teak (Moret et al. 1998, Bermejo et al. 2004, Pérez & Kanninen 2005, Tewari et al. 2013, Malimbwi et al. 2016, Subasinghe 2016, Zahabu et al. 2018, Aguilar et al. 2019, Kenzo et al. 2020). These models are as follows:

$$vob = \alpha + \beta(dbh)^2(Ht) \tag{5}$$

$$vub = \alpha + \beta(dbh)^2(Ht) \tag{6}$$

$$vob = \alpha[(dbh)^2 (Ht)]^{\beta} \tag{7}$$

$$vub = \alpha[(dbh)^2 (Ht)]^{\beta} \tag{8}$$

Stand volume and above-ground biomass equations

Allometric stands models were used to model: volume over bark (*VOB*), the volume under bark (*VUB*), and above-ground biomass (*B*). These variables are expressed in $m^3 \cdot ha^{-1}$ for volume and in megagrams per hectare ($Mg \cdot ha^{-1}$) for biomass. Using the best model for individual trees (*vob*, *vub*, and *b*), these variables were estimated for each tree in each PSP census, and the basal area also estimated per individual tree. The same procedure was carried out for the trees thinned in each plot based on the *dbh* of each tree before thinning.

For *VOB*, *VUB*, and *B*, per plot, the same variables for the surviving trees in each census were added to each plot. The results were linearly scaled to a hectare to obtain *VOB*, *VUB*, the basal area in $m^2 \cdot ha^{-1}$ (*G*), and *B*. To fit the allometric models for the stands, *VOB*, *VUB*, and *B* were used as dependent variables of *G*, as has been suggested by García (2013a, 2013b). Because the variables calculated for each yearly PSP census can exhibit autocorrelation, the models:

$$VOB = \alpha_1 G^{\beta}{}_1 \tag{9}$$

$$VUB = \alpha_2 G^{\beta}{}_2 \tag{10}$$

$$B = \alpha_3 G^{\beta}{}_3 \tag{11}$$

where: α_i and β_i are the parameters to be estimated, were fitted using nonlinear mixed-effect-models (NLMEMs) (Fang et al. 2001) to evaluate two types of variance in the independent variable, the proportional variance to the mean and the variance as a potential function of the mean. The two resulting models for each independent variable were evaluated according to the statistical significance of the parameters and compared with the Akaike Information Criterion (*AIC*) and the Bayesian Information Criterion (*BIC*) to choose a single equation for each variable.

Modeling yield in volume and above-ground biomass per hectare

The SSA was used to model the production of the stands (García 1994, 2013a, 2013b). In this approach, the system behavior is described by a one-dimensional state vector represented by *G* and three output functions representing *VUB*, *VOB*, and *B*. The transition function for *G* is analytically determined as follows: (i) a growth model for the gross basal area (G_g) is adjusted, (ii) this function is derived with respect to time, (iii) G_g is explicitly expressed in the differentiated model and (iv) the model obtained in the previous step is integrated (Figure 2).

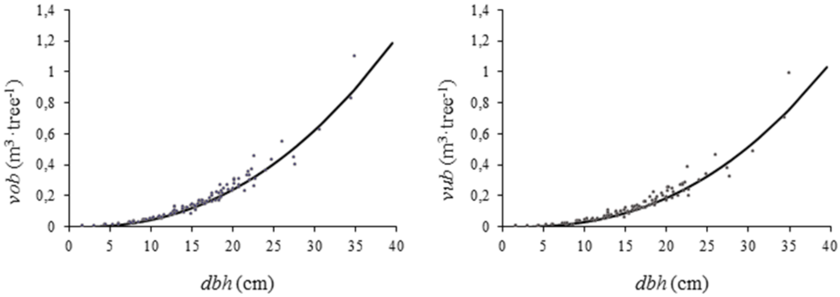
Here, G_g is determined as follows: in the thinned plots, the basal area of thinned trees is added to the basal area of living trees in the post-thinning measurements. In non-thinned PSPs, the basal area of the surviving trees corresponds to G_g. This procedure allows an estimation of the carrying capacity of the stands, and the continuous evolution of G_g over time for each plot could be obtained. For the yield function of G_g, von Bertalanffy's (Vanclay 1999) and Kopf's (Kiviste et al. 2002) models were evaluated:

$$G_g = A[1 - exp(-\beta_1)t]^{\beta}{}_2 \tag{12}$$

$$G_g = A\, exp[-(\beta_1/t^{\beta 2})] \tag{13}$$

where: *A* is the asymptote, *exp* is the base of the natural logarithms (*e*), and β_1, β_2, and β_3 are parameters to be estimated. By anticipating the existence of autocorrelation, the models were restructured and fitted as NLMEMs:

$$G_g = \beta_1 \left[\frac{1 - \exp(-\beta_2 t)}{1 - \exp(-\beta_2 t_0)} \right]^{\beta_3} \tag{14}$$



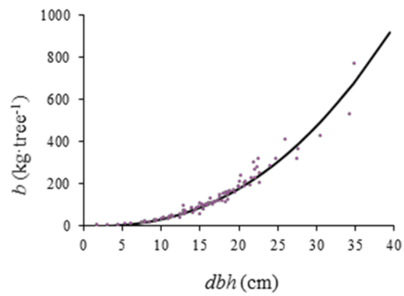


Figure 2
Individual tree allometric models for the volume over bark (*vob*) volume under bark (*vub*), and biomass (*b*), depending on diameter at breast height (*dbh*). Estimated (solid lines), observed values (dots).

$$G_g = \beta_1 \exp\left[-\beta_2\left(\frac{1}{t^{\beta_3}} - \frac{1}{t_0^{\beta_3}}\right)\right] \qquad (15)$$

where: $\beta_1 = ø + b$. Here β_1 is considered a mixed parameter: one part with a constant value ($ø$) and the other with a random value (b), β_2 and β_3 are unknown but fixed parameters in both models. Note that when $t = t_0 = 12$, the gross basal area at the base age of 12 years corresponds to the site index curves used here (Torres et al. 2012). These site index curves were calculated in the same teak plantations of this study, and currently, the only one published for this species in Colombia.

Models (14) and (15) were fitted in SAS (2004) assuming β_1 as a single random effect parameter. For each model, three variance structures were considered: a constant, a potential function of the mean, and an exponential function of the mean. Each model was evaluated based on: (i) the statistical significance of the parameters and (ii) the *AIC* and the *BIC* statistics. After the model was selected, it was derived, written explicitly for G_g, and integrated, which gave rise to a model for G_g that represents the state of the system at any moment in time. Finally, the value of the parameter β_1 corresponding to the value of the G_g reached in the base age t_0 will depend on the site quality, so a regression between site quality and β_1 was carried out to obtain yield curves as a function of age and site quality.

As the model (15) was selected (see in results eq. 26 and Table 4), the first derivative of the model (15) respect to time (t) is:

$$\frac{dG_g}{G_g dt} = \left(\beta_2 \beta_3 \frac{t^{-\beta_3}}{t}\right) \qquad (16)$$

By writing G_g explicitly on the right-hand side of the eq. (16) gives:

$$\frac{dG_g}{dt} = \frac{\beta_3 \cdot G_g}{t}\left[\ln(\beta_1) - \ln(G_g) + \beta_2 t_0^{-\beta_3}\right] \qquad (17)$$

The rearranging of eq. (17) for integration, gives eq. (18):

$$\frac{dG_g}{\beta_3 G_g\left[\ln(\beta_1) - \ln(G_g) + \beta_2 t_0^{-\beta_3}\right]} = \frac{dt}{t} \qquad (18)$$

Integrating both sides of eq. (18) between G_{g1}

and G_{g2} and between t_1 and t_2 gives the transition function (eq. 19):

$$G_{g2} = \exp\left[\ln(\beta_1) - \frac{\left\{ \left[\ln(\beta_1) - \ln(G_{g1}) \right] t_0^{\beta_3} + \beta_2 \right\} \left(\frac{t_1}{t_2} \right)^{\beta_3} - \beta_2}{t_0^{\beta_3}} \right]$$

(19)

In eq. (19), G_{g1} corresponds to the basal area at age t_1, and $G_{g1} < G_{g2}$. Other terms are equal to those of the original eqs. (15) and (26). In each PSP G_g involves the basal area of the living trees at time t_2 plus the basal area of thinned trees at age t_1, if there were thinnings; therefore, the G_{g2} values at any age t_2 reflect the current basal area of the stand plus the basal areas of all previous thinnings.

Results

Volumes and above-ground biomass equations for individual trees

A sample of 102 trees was collected that covered the entire range of age classes and diameters of the PSPs, as shown in Table S1 (Supp. Info.). Table S2 (Supp. Info.) presents the statistical results of fitted models (2) to (4) with different weights before the validation. The fits of the un-weighted models (weighting multiplied by 1) are highly significant ($R^2 > 0.94$, $p < 0.0001$) for all cases. But, in these models, the variance is not homogeneous (*B-P* test, $p < 0.05$), and errors are not normally distributed (*S-W* test, $p < 0.05$). The same models were fitted by weighted least squares, resulting in all models that the best weighting was the inverse of the absolute value of the residuals (1/abs(e), where e is the error). In the weighted models, the fits are also highly significant, but the proportion of the variance in the dependent variable predictable from the independent variable is much higher ($R^2 > 0.99$, $p < 0.0001$). They meet two regression assumptions for $\alpha \leq 0.05$, but some heteroscedasticity persists, Table S2 (Supp. Info.). Figure S1 (Supp. Info.) shows the residuals obtained with each model, both for the data used to fit the models (self-validation) and for the independent data (independent validation). The variations of the estimates in the independent data are within the natural range variation of the data used to fit the models. Table 1 presents the values for the mean absolute difference, mean relative difference, and model efficiency for both data sets. The criteria in Table 1 show the suitability of the models with efficiencies above 92%. The mean absolute and relative differences in the independent data are smaller than those calculated for the data used for model fitting. The only exception is the model for *b*, whose mean relative difference for the model data was slightly smaller than those for the independent data. The mean absolute difference for *b*, for both self-validation and independent validation, was much higher (15.91 and 14.97, respectively) than for *vob* and *vub* (from 0.016 to 0.022). Therefore, for this criterion, both validations for *b* are much less satisfactory than for *vob* and *vub* (Table 1 and Table S2, Supp. Info.). Figure 2 and eqs. (20) to (22) show the models that were previously validated and calibrated with all the data:

$$vob = 0.000228(dbh)^{2.326409} \quad (20)$$

$$vub = 0.000113(dbh)^{2.48705} \quad (21)$$

$$b = 0.131748(dbh)^{2.406413} \quad (22)$$

For the eqs. 20 to 22, the *D-W* statistic for $\alpha = 0.05$ does not reject the null hypothesis of no first-order autocorrelation (Table S2, Supp. Info.).

The results of fitting the models 5 to 8 are presented in Table 2. The goodness of fits of both linear and allometric models with combined variables explain a high proportion of the variances ($R^2 > 0.81$, $p < 0.0037$ for linear models, and $R^2 > 0.97$, $p < 0.0001$ for allometric models), and their parameter estimators are above the 95% confidence level. However, they are lower than those of eqs. (20) to (22) ($R^2 > 0.99$, $p < 0.0001$), do not conform to assumptions of normality of errors (*S-W* test, $p < 0.05$), and homoscedasticity of errors (*B-P* test, $\alpha < 0.05$). The linear-combined variable models have positive autocorrelation of errors (*D-W* test, $\alpha = 0.05$), which is complicated by the fact that they involve the measurement of an additional variable.

Stand volume and above-ground biomass equations

The parameter estimators of models 9 to 11 evaluated on each of the variance structures were statistically significant, with confidence levels over 95%. Table 3 shows the values of the two selection criteria that took each of the models under the two types of variance structure. Although all models were statistically similar according to the *AIC* and *BIC*, the models with variances proportional to the mean are the most suitable for *VUB* and *B* (lower values for *AIC* and *BIC*, in eq. (10.1) and (11.1); but not in *VOB* in which the variance as a potential function of the mean is better (eq. 9.2 in Table 3). The fitted models are shown in Figure 3, whose equations are:

$$VOB = 3.7468G^{1.2289} \tag{23}$$

$$VUB = 2.4414G^{1.2664} \tag{24}$$

Table 1 Self-validation and independent validation of the individual trees allometric equations are presented for *vob* (volume over bark, m^3), *vub* (volume under bark, m^3), *b* (biomass, kg) using three criteria for validation: mean absolute difference $(\sum|\hat{y}_i - y_i|/n)$, mean relative difference $(100[\sum|\hat{y}_i - y_i|/|y_i|]/n)$ and model efficiency $(1-[\sum(y_i-\hat{y}_i)^2/\sum(y_i-\bar{y})^2])$ Self-validation was calculated with the 85 trees used to fit the allometric regression. Independent validation with 17 randomly selected trees not used in the regressions.

Models	Equation 2 (*vob*)		Equation 3 (*vub*)		Equation 4 (*b*)	
Validation criteria	Self-validation	Independent validation	Self-validation	Independent validation	Self-validation	Independent validation
Mean absolute difference	0.022	0.016	0.021	0.018	15.912	12.467
Mean relative difference %	11.904	10.750	17.074	15.187	17.467	18.612
Model efficiency	0.956	0.945	0.941	0.922	0.953	0.944

Table 2 Statistical results of volume over bark (*vob*) and volume under bark (*vub*) models for individual trees as a function of the combined variable. Linear-combined *vob* or *vub* = $\alpha + \beta(dbh)^2(Ht)$, allometric- combined *vob* or *vub* = $\alpha[(dbh)^2(Ht)]^{\beta}$.

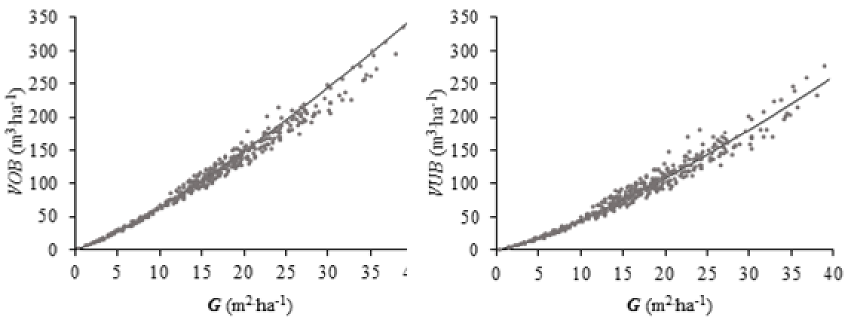
Models	Variable	Parameters[a]		Verification of assumptions[b]			
				p			
		α	β	R^2	*D-W*	*S-W*	*B-P*
Linear-combined variable	*vub*	-2.19022	0.000072	0.8184	1.002	0.0029	3.271
				0.0023	$<0.05^{+}$	$<0.05^{n}$	$<0.05^{h}$
	vob	-2.45201	0.000076	0.8385	1.008	0.0064	3.447
				0.0037	$<0.05^{+}$	$<0.05^{n}$	$<0.05^{h}$
Alometric-combined variable	*vub*	0.000049	0.953645	0.9782	1.900	<0.0001	26.78
				<0.0001	<0.05	$<0.05^{n}$	$<0.05^{h}$
	vob	0.000021	1.021213	0.9708	1.922	<0.0001	27.59
				<0.0001	<0.05	$<0.05^{n}$	$<0.05^{h}$

Note. [a]Parameter estimators: in all models, the parameters are over 95% confidence level. [b]R^2 fitting for degrees of freedom. Durbin-Watson test (*D-W*, $\alpha = 0.05$) for autocorrelation of the errors, $^{+}$ positive autocorrelation. Probability value for testing normality of the errors, Shapiro-Wilk test (*S-W*, $\alpha = 0.05$), *n* - not normally distributed. Conditional number and probability value for heteroscedasticity test of errors, Breusch-Pagan test (*B-P*, $\alpha = 0.05$), *h* - heteroscedasticity.

Table 3 Values of the criteria Akaike Information Criterion (*AIC*) and Bayesian Information Criterion (*BIC*) for selecting stand-level allometric models are presented (eqs. 9 to 11). Two variance structures in the independent variable are included (proportional, eqs. 9.1 to 11.1, and potential, eqs. 9.2 to 11.2): *VOB* (volume over bark, $m^3 \cdot ha^{-1}$), *VUB* (volume under bark, $m^3 \cdot ha^{-1}$), *B* (biomass, $Mg \cdot ha^{-1}$). The models selected in bold.

	Equation 9 (*VOB*)		Equation 10 (*VUB*)		Equation 11 (*B*)	
	9.1	9.2	10.1	10.2	11.1	12.2
Variance structure	Proportional	Potential	Proportional	Potential	Proportional	Potential
*AIC**	2403.8	**2273.6**	**2477.6**	2496.5	**2379.0**	2410.2
*BIC**	2411.0	**2280.7**	**2484.7**	2503.7	**2386.4**	2417.6

Note. * The smaller the value, the better the model.



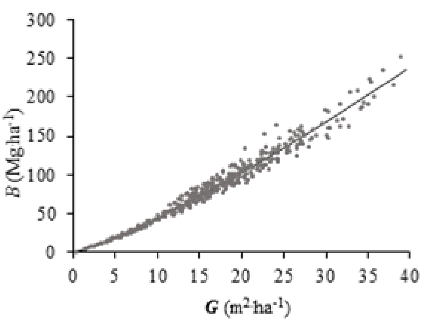


Figure 3

Stand allometric models for the volume over bark (*VOB*) volume under bark (*VUB*), and biomass (*B*), depending on the basal area (*G*). Estimated (solid lines), observed values.

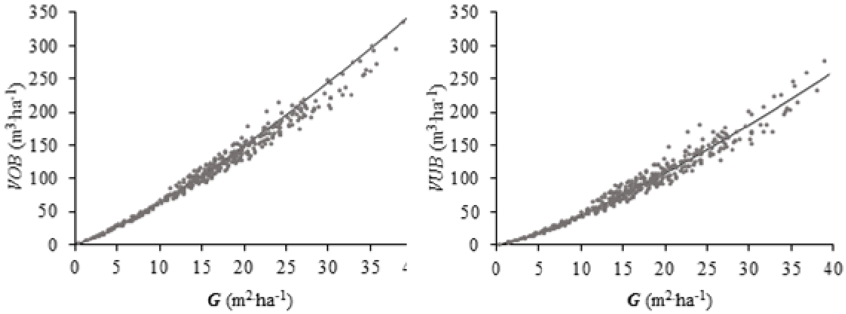
$$B = 2.6342G^{1.2225} \qquad (25)$$

Modeling of volume and above-ground biomass yield per hectare

The parameter estimators of models (14) and (15) evaluated in each of the variance structures were statistically significant, with confidence levels over 95%. Table 4 presents the values of these parameters and the selection criteria. Both models were statistically similar for *AIC* and *BIC*, but Kopf's model (15) with constant variance in G_g (eq. 15.1 in Table 4), was the best:

$$G_g = 27.8084exp\left[0.5090 - \frac{4.9664}{t^{0.9167}}\right] \qquad (26)$$

Keeping in mind that β_1 (eq. 15) is a mixed-effect parameter that represents the random effect of environmental variability related to site quality. The value of this parameter represents the basal area attained at the base age t_0= 12 years and $\overline{Hd}$ = 17.3 m (eq. 1). Then, 27.8084 $m^2 \cdot ha^{-1}$ (eq. 26) is the average basal



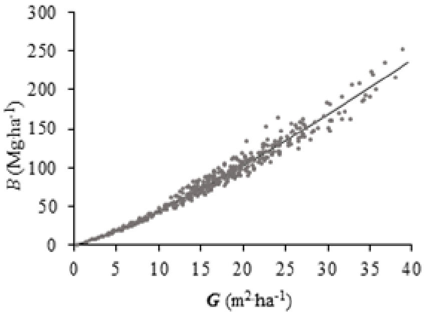


Figure 3
Stand allometric models for the volume over bark (*VOB*) volume under bark (*VUB*), and biomass (*B*), depending on the basal area (*G*). Estimated (solid lines), observed values (dots).

Table 4 Parameter estimators' β_1, β_2, and β_3 of the two growth models (von Bertalanffy and Kopf) for the basal area (G_g) depending on age (t in years) fitted using three variance structures. The fitting criteria were: Akaike Information Criterion (*AIC*) and Bayesian Information Criterion (*BIC*). In bold, the criteria and parameter estimators of the model selected.

Models		Equation 14 (von Bertalanffy)			Equation 15 (Korf)		
		14.1	14.2	14.3	15.1	15.2	15.3
Variance structure		Constant	Potential	Exponential	Constant	Potential	Exponential
*AIC**		1604.9	1629.6	1668.1	**1582.7**	1609.4	1703.3
*BIC**		1613.6	1638.3	1676.8	**1591.4**	1618	1672.1
Parameter estimators	β_1	27.575	27.7049	28.1637	**27.8084**	27.4084	27.5321
	β_2	0.2158	0.2173	0.2079	**4.9664**	4.9428	4.9260
	β_3	1.9415	1.9939	1.9729	**0.9167**	0.908	0.8826

Note. * The smaller the value, the better the model.

area ($m^2 \cdot ha^{-1}$) reached by the PSPs with mean site index at age 12 (17 PSPs classified in site index class 3, Figure S2 (Supp. Info.).

Model fitting, validation, and calibration

The transition eq. (19) meets the properties of consistency, composition, and causality (García 1994): consistency, because if no time has elapsed, there will be no change in state; that is, if $t_1 = t_2$, then $G_{g1} = G_{g2}$. Composition or semigroup property; the results of projecting the state from t_0 to t_1 and then from t_1 to t_2 are the same as the projection from t_0 to t_2. Causality, referring to the change of state, that can only be influenced by the entries in the time interval considered; then, if the previous thinnings were not added, the model will underestimate the total yield. The parameter β_1 in the Kopf's model (which is G_g at the base age t_0 = 12 years) is directly related to site quality. Therefore, a linear regression model fitted for β_1 depending on site index classes (*SIC*) of each PSP results in the negative linear regression (eq. 27):

$$\beta_1 = 52.5100 - 8.8113(SIC) \quad (27)$$

with $r^2 = 0.8575$ ($p < 0.001$) (Figure S2, Supp. Info.). It allows transition functions for different *SIC* (from 1 to 5) by only varying the value of the parameter β_1. The output functions obtained in the previous phase, namely, the stand allometric models, are presented in eqs. (23) to (26), which can be used to estimate these variables from the current basal area value at a given time. There are three ways to obtain the basal area: (i) by direct measurement in the field, or calculating it from PSPs, (ii) estimating it with the growth eq. (25), (iii) estimating it with the transition eq. (19), and β_1 with eq. (27). Figure 4 shows the trends of the system over time for each site index class, and the basal area used in the output function estimated with eqs. (19) and (27).

Yield curves for *VOB*, *VUB*, and *B* for each site index class

When the transition eq. (19) is used to predict the behavior of the system, an infinite number of possible combinations may exist. Figure 5 shows some possible system responses when thinnings are performed for three site index classes (1, 2, and 3). In this example, G_{g2} is estimated by using eq. (19). Then, 30% thin-

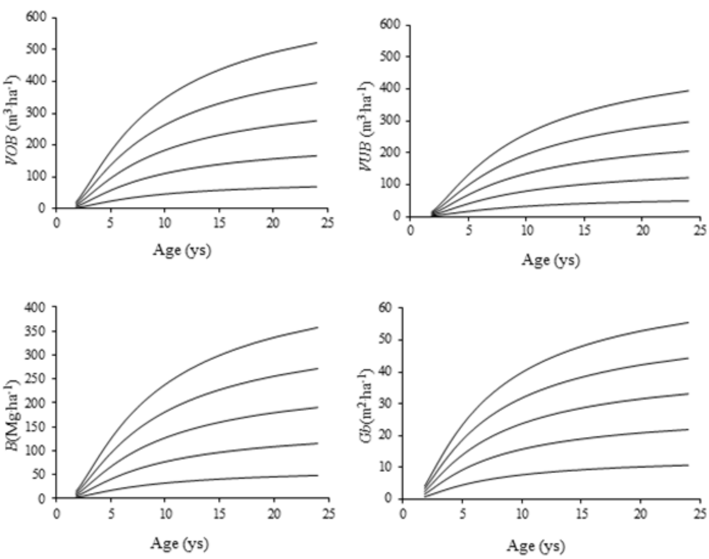


Figure 4 Yield curves for volume over bark (*VOB*), the volume under bark (*VUB*), biomass (*B*) and basal area (G_g) depending on age for the five site index classes (*SIC*) found in the study area. The yield functions were estimated with the transition function (eq. 19): β_1 (eq. 27), β_2 = 4.9664, β_3 = 0.9167 (Table 4). β_1 is the basal area at base age 12 depending on *SIC* at the same age: *SIC* 1 with dominant height ($\overline{Hd}$) at age (t_0) 12 = 23.3 m, and β_1 = 43.8 m²·ha⁻¹; *SIC* 2 with $\overline{Hd}$ = 20.3 m, and β_1 = 34.9 m²·ha⁻¹; *SIC* 3 with $\overline{Hd}$ = 17.3 m, and β_1 = 26.1 m²·ha⁻¹; *SIC* 4 with $\overline{Hd}$ = 14.3 m, and β_1 = 17.3 m²·ha⁻¹; *SIC* 5 with $\overline{Hd}$ = 11.3 m, and β_1 = 8.5 m²·ha⁻¹.

nings of G_{g1} are simulated at years 4, 6, and 9 (t_2 ages), and a final thinning of 15% of G_{g1} at age 15. Finally, the values of G_g, those thinned and retained, were replaced by *VOB*, *VUB*, and *B* using the system's output eqs. (23) to (25) to obtain volumes and biomasses thinned and retained. In Figure 5, only the results of *VOB* and *B* are presented.

Discussion

In all cases, based on the criteria employed, nonlinear regression weighted by the inverse of the absolute value of the residuals, self-validation, independent validation, recalibration, and meeting the regression assumptions, the simple allometric models of *b*, *vub*, and *vob* as a function of *dbh* (eqs. (20) to (22) (Table 1, and Table S2, Supp. Info.), were statistically better than other popular models (Table 2), such as the combined variables (dbh^2Ht) and compound allometry ($\alpha[(dbh)^2(Ht)]^\beta$) used in most previous teak studies. Similar results have been reported in India for *b* (Buvaneswaran et al. 2006). The percentage of variance explained by our simple allometric models for *vob* and *vub* was 99.14% and 99.51%, respectively (Table S2, Supp. Info.). Therefore, other models with more variables and that to a lesser degree satisfy the regression assumptions, and that only explain between 81.84% and 97.82% of the variances are not justified to be used in this paper. From the statistical point of view, the main problem with the linear combined variable used in some volume equations is the autocorrelation of the errors. Unlike of the methods suggested estimating the volume and biomass of teak that including as independent variables, *dbh*, and *Ht* (Bohre et al. 2013, Koirala

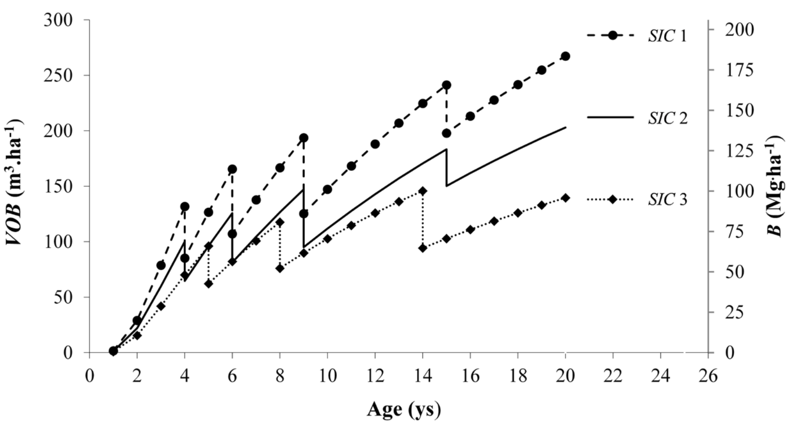


Figure 5 Stand's simulations of thinning´s yield treatments and final harvest at age 20 for volume over bark (*VOB*) and above-ground biomass (*B*) for site indexes classes (*SIC*): 1, 2, and 3. In this example, G_{g2} is estimated by using eq. (19): β_1 is eq. (27), β_2 = 4.9664, β_3 = 0.9167 (Table 4), and t_0 the base age 12. Then 30% thinnings of G_{g1} were simulated at years 4, 6, and 9 (t_2 ages), and a final 15% thinning of G_{g1} was simulated at age 15. Finally, the values of G_g thinned and retained were replaced by *VOB* and *B* using the system's output eqs. (23) and (25) to obtain volumes and biomasses thinned and retained. *SIC* 1 with dominant height ($\overline{Hd}$) at age (t_0) 12 of 23.3 m, and β_1 = 43.8 m²·ha⁻¹ (eq. 27); *SIC* 2 with $\overline{Hd}$= 20.3 m at age 12, and β_1 = 34.9 m²·ha⁻¹; *SIC* 3 with $\overline{Hd}$ = 17.3 m at age 12, and β_1 = 26.1 m²·ha⁻¹.

et al. 2017), that are auto-correlated because trees with larger diameters tend to have greater heights (Tewari & Singh 2018b), it could be believed that the combined variable dbh^2Ht works as a single variable, and there should be no autocorrelation; however, our data says otherwise, there are positive autocorrelations in our volume and biomass equations that included this linear combined variable (Table 2). Among all the regression assumptions, autocorrelation is the most inviolable for statisticians because it means that the variables are not really independent.

Regarding the models with compound allometry, in our study, they did not show autocorrelation (Table 2). But it cannot be ruled out that, in other previously published studies, there has been autocorrelation. In the studies examined, the authors focus mainly on the goodness of fit, but neglect compliance with the regression assumptions. Note that a regression model is not discarded by the low statistical adjustment, as this is not a regression assumption. Chaturvedi & Raghubanshi (2016) studied the marginal gain when calculating the volume of teak using simple allometry with *dbh* in teak, compared to the composite allometry $\rho(dbh)^2Ht$, were ρ is wood density; they concluded that "it should be determined whether it is biologically relevant to take efforts to measure ρ and/or *Ht* for a small gain in the performance of the model".

The equations used by most authors only include *vob*, but nor *b* neither *vub*. Only the study by Jerez et al. (2015) includes these three variables but based on volume and biomass equations taken from the literature that neither verify compliance with the regression assumptions nor were independently validated. Most models used for teak explain less variance, are less parsimonious, or do not have corrected the bias induced by the logarithmic transformation (Moret et al. 1998, Bermejo et al. 2004, Keogh 2005, Pérez & Kanninen 2005, Watanabe et al. 2009, Sreejesh et al. 2013, Tewari et al. 2013, Sandeep et al. 2015). The first correction for this bias dates from more than 80 years ago (Meyer 1938, 1941, Picard et al. 2012). Satoo (1982) reviewed all the proposals to correct the logarithmic bias; so far, there is no new proposal. We found that this bias has been appropriately corrected only in a few teak investigations (Sunanda & Jayaraman 2006, Mbaekwe & Mackenzie 2008, Guendehou et al. 2012, Tewari et al. 2014, Tewari & Singh 2018a). Our self-validation, independent validation, and recalibration protocol ensure that there are no biases when we estimate tree volumes or biomass with eqs. (20) to (22) because these values correspond to the arithmetic mean, and not the geometric mean of the logarithmic transformation, which always is less than the arithmetic mean. In the reviewed literature, we find that the volume and biomass equations for teak trees have never before been independently validated. In this regard, it is worth recording what Denis Alder wrote 40 years ago: "A model which is not validated is simply speculation and guesswork" (Alder 1980).

The stand eqs. (23) to (25) are useful for a rough but rapid estimation of *VOB*, *VUB*, and *B* depending on *G*. Note that they depend neither on age nor on *SIC*, as previously suggested by García (2013a, 2013b). But, for a more precise estimation of these yield variables depending on age and *SIC*, eqs. (19), and (27) must be used because the values of G_{g2} also depend on the *SIC*, according to the β_1 values (eq. 27 and Figure S2, Supp. Info.). As a result, for the same basal area, the higher the *SIC* at any age *t*, the greater the values of *VOB*, *VUB*, and *B* when G_2 is replaced in eqs. (23) to (25).

The allometric stand models fit very well when *G* is used as a predictor, and this result allowed yield to be modeled with the SSA because a single state variable was generated (eq. 19). Therefore, the transition function is expressed one-dimensionally. The production model is shown by the transition function (eq. 19), after inserting the NLMEMs eq. (27) of *SIC* and the output eqs. (23) to (25) can estimate the stand yield in *VOB*, *VUB*, and *B*. Also they allow simulating thinnings regiments for any *SIC*, in which the variable reflecting the change of state is *G* (Figure 4). In contrast, usually, the methods based on the SSA currently used for teak and other species would typically require at least two transition equations for variables such as *SI*C (or some variable related to trees height) and *G* (García 1994, 2013a, 2013b, Nord-Larsen & Johannsen 2007, Quintero 2012, Tewari et al. 2014, Jerez et al. 2015, Tewari & Singh 2018). Adding the thinned basal area in G_1 to the transition function (eq. 19) ensures that total yield in *VOB*, *VUB*, and *B* have not been underestimated, as it usually happens in thinned temporal sampling plots (Phillips 1995), and when a mixture of thinned temporary sampling plots and thinned PSPs are used, especially when the thinned volumes and biomasses have not been added to the transition function (Jerez et al. 2015).

Among the 74 growth equations compiled by Kiviste et al. (2002) to study growth and yield in forest plantations, few of them, including the two used here (Kopf & von Bertalanffy), contain a parameter for the shape of the curve. In many of them, not a shape parameter exists, and the change of concavity occurs at a fixed proportion of the asymptote, unrelated to the database used. In particular, for Kopf's equation, this parameter is β_3 = 0.9167 in this study (Table 4).

Some authors have calculated simulations of thinnings for teak using PSPs, but only for *VOB* (Zambrano et al. 1995, Quintero et al. 2012). Jerez et al. (2015) simulate thinnings for *VOB*, *VUB*, and *B* using thinned plots, both temporary and permanent. Phillips (1995) simulates the thinnings and the final yield for *VOB* based on temporary plots. Other authors that used temporary plots, explicitly express that they could not carry out thinnings simulations because they underestimate total yield (Nunifo & Murchinson 1999, Sunanda & Jayaraman 2006).

As far as we know, the only four studies of teak growth and yield that had used the SSA are Quintero et al. (2012) and Jerez et al. (2015) in Venezuela, and two studies in India (Tewari et al. 2014, Tewari & Singh 2018a). The two studies from India are methodologically the same. The only difference we find between them is that Tewari et al. (2014) employed 22 PSPs of different sizes so that 30 trees can fit on them. These PSPs have been measures for three consecutive years. In contrast, Tewari & Singh (2018a) used only fifteen of the same PSPs. The two studies from India estimate the *VOB* yield in non-thinned plots at any time, and they included a mortality function. In these studies the autocorrelation from successive measurements was removed. They do not include thinnings simulations. The two studies from Venezuela are also methodologically very similar. Quintero et al. (1995) used non-thinned PSPs to simulate *VOB*, and Jerez et al. (2015) used a mixed of thinned temporal and PSPs to simulate *VOB*, *VUB*, and *B*. They did not filter the temporal autocorrelation and did not verify compliance with the regression assumptions in their models.

In this study, we did not calculate a natural mortality function. Natural mortality is significant in non-thinned stands, as in the studies from India (Tewari et al. 2014, Tewari & Singh 2018a) and Venezuela (Quintero et al. 2012). But no in this study because most of our PPPs, have been thinned, and natural mortality was virtually non-existing. In this paper, we remove autocorrelation with NLMEMs. As far as we have searched on the teak literature, no previous research addresses the here fulfilled objectives in a single document.

Pérez & Kanninen (2005) have found that teak tends to have higher growth rates in the Neotropics than in the Paleotropics. This fact was confirmed by the comparisons made by Khanduri & Vanlalremkimi (2008) in India, who found that the yields reported by Pérez and Kanninen (2005) for Costa Rica were among the highest in the literature, although lower than the 33.45 $m^3 \cdot ha^{-1} \cdot year^{-1}$ mean *VOB* annual increment at year 20 reported for Tuirial, India. Our *SIC* 1 for *VOB* at 20 years (491 $m^3 \cdot ha^{-1}$) is comparable with the best site of Pérez & Kanninen (2005). Tewari & Álvarez-Gonzáles (2014) developed a stand density management diagram for teak plantations in Southern India. At age 20, our *SIC* 1 and *SIC* 3 for *VOB* are over the predicted yields for India. In contrast, our *SIC* 5 is well under the less productive site of India. So, this study includes sites that represent the best and worst *SICs* for teak reported in the literature, showing the urgent need to assess site quality before planting to avoid the less productive sites.

Conclusions

We have presented compatible growth and yield equations for teak in the Colombian Caribbean. The models predict growth and yield in terms of basal area, volumes (over bark and under bark), and above-ground biomass as a function of age and site index classes. For the first time in teak, the method presented here enables the simulation of thinnings and total yield for these variables, by avoiding biases reducing total yield: (i) not to correct the bias of the logarithmic transformation of the allometric tree equations and (ii) not adding the thinnings yields to the total yield in the transfer function. Our equations for tree volumes and biomass were self-validated, independently validated, and recalibrated.

We used a novel and more parsimonious sta-te-space approach. Previous researches in teak usually need a transition function for basal area and other transition function for dominant trees height. But in our approach, we only needed a single transition function for these two varia-bles. By using a non-linear mixed-effects-mo-del equation, we incorporated the unknown parameter $\beta_1 = ø + b$, which corresponds to the gross basal area at the site index base age. It is composed of a constant (fixed) value ($ø$) and a random value (b), inserting into Kopf's growth model for the basal area. The parameter β_1 re-sults in a negative linear function depending on site index classes ($r = –0.9260$, $p < 0.001$) from the best (site index class 1) to the worst (site index class 5). Thus, β_1 is inserted for site quality in the transition function for the basal area.

Our method overcomes most of the drawbacks previously found in some growth and yield studies for teak: statistical assumptions of the independence of variables, autocorrelation and normality of residuals, heteroscedasticity, biases, and different metrics. We believe that our results can be used to estimate the yield of young plantations for all the variables that we studied and potentially to simulate the effect of thinnings in other parts of the tropics where little information is available.

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Supporting Information

The online version of the article includes Supporting Information:

Figure S1. Dispersion of the residuals

Figure S2. It shows the linear relationship between theβ1 parameter and site index classes

Table S1. Summary of characteristics of the sampled trees

Table S2. Statistical results of fitting allometric models for individual trees