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Individual-tree growth and mortality models for a semideciduous Atlantic forest in Brazil

[1]Carlos Pedro Boechat Soares, [2]Salvador Alejandro Gezan, [3]Gilson Fernandes da Silva, [4]Renato Vinícius Oliveira Castro

[1]Departamento de Engenharia Florestal, Universidade Federal de Viçosa, Avenida P.H. Rolfs, s/n - Campus UFV. Post Code: 36570-900 Viçosa, MG, Brazil.
[2]School of Forest Resources and Conservation, University of Florida, PO Box 110410. Gainesville, FL, Post Code: 32611-0410.
[3]Departmento de Engenharia Florestal, Universidade Federal do Espírito Santo, Av. Governador Lindemberg, 316 – Centro, Post Code: 29550-000, Jerônimo Monteiro, ES, Brazil.
[4]Departamento de Ciências Agrárias, Universidade Federal de São João del Rei, Campus Sete Lagoas, MG 424, Km 47, Sete Lagoas, MG, Brazil, Post Code: 35701-970.

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ABSTRACT

The objectives of this study were to identify important stand and tree variables that help to: explain the response on growth and mortality of tree species from a semideciduous Atlantic Forest; construct models that predict periodic annual increment in diameter (PAI_d), height-diameter relationship and probability of mortality (P(M)); and, evaluate different statistical fitting methodologies for the construction of diameter growth models. Data from permanent plots (20 x 50 m) measured in 1994, 1997, 2000, 2004 and 2008, located at the municipality of Viçosa, Minas Gerais State, Brazil, were used for analyses. The explanatory variables most significant ($p<0.05$) to predict PAI_d, height-diameter relationship and *P(M)* were *dbh*; inverse of *dbh*; total height (H_t); maximum *dbh* (D_{max}); basal area per hectare of trees larger than subject tree (*BAL*); and average height of dominant trees (H_d). The PAI_d model was fitted using traditional methodology, but the inclusion of random intercepts and slopes within the framework of linear mixed models resulted in important gain in precision for most of predominant species. The height-diameter models fitted well to the observed data by the use of nonlinear regressions and the fitting of a logistic model to predict probability of mortality provided with moderate precision of estimates of dead trees for most periods, however, this did not affected the estimation of basal area per hectare for any period.

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INTRODUCTION

The Atlantic Forest in Brazil it is recognized as one of top five world's hotspots containing endemic plants and vertebrates amounting to world-wide at least 2% of the total species (Myers *et al*., 2000) and it was one of the largest mixed forests in the world covering nearly 150 million hectares. However, due to deforestation, at the present, only 9% of the original area of these forests exist (MMA, 2007).

In addition to laws that regulate the use of forests in Brazil through sustainable forest management practices, other alternatives have been implemented to reduce deforestation such as Reducing Emissions from a Deforestation and Degradation (REDD) projects and valuing environmental services as carbon sequestration (Wunder, 2007).The implementation of any of these initiatives requires a detailed knowledge of the current stock, which is typically obtained through forest inventories, and the future stock by the growth and yield models (Salimon *et al*., 2011).

There are many types of growth and yield models to predict carbon (and/or volume) stock (Davis and Johnson, 1987), such as stand, class and tree level models. According to Weiskittel *et al*. (2011) the latter are the most appropriate for natural mixed forest as they have the ability to describe complex stand structures and to ensure reliable predictions for a range of tree sizes, sites and stand conditions (Zhao *et al*., 2004) as the tropical forests. These tree level models usually consist on diameter and height increment functions that depend on several stands and tree variables together with a mortality equation used to predict individual tree probability of mortality. In addition, for natural forests, a regeneration or ingrowth routine to recruit new trees often is implemented (Hasenauer, 2006).

Tree level models are traditionally fitted by linear and nonlinear regressions using repeated

Corresponding Author: Carlos Pedro Boechat Soares, Departamento de Engenharia Florestal, Universidade Federal de Viçosa, Avenida P.H. Rolfs, s/n - Campus UFV. Post Code: 36570-900 Viçosa, MG, Brazil.

measurements originated from permanent plots, and therefore, basic residuals assumptions need to be considered in the fitting process, such as temporal correlations and heterogeneity of variances (Gujarati, 2002; Calegário *et al*., 2005). Different statistical techniques can be considered in the estimation of parameters that incorporate these aspects, such as linear and nonlinear mixed models, generalized linear mixed model and simultaneous equations (Zhao *et al*., 2004).

In Brazil, few studies on the modeling of the growth at individual tree level in natural forests from different biomes exist (Phillips *et al*., 2004), where some models, of limited use, were developed for specific native species in the Atlantic Forest (Durlo, 2001; Nutto, 2001; Durlo *et al*., 2004) and other for species from the Amazon (Silva *et al*., 2002; Della-Flora *et al*., 2004). The calibration of dynamic models for wider application requires repeated tree observations and permanent plots covering a wide range of stand densities, forest and soil types, ages (Hasenauer, 2006) and specially for tropical forests, different succession stages. In addition, other elements might need to be included to improve the explanatory power of the models such as topography (Hasenauer and Monserud, 1997) and random events such as pathogens, snow storms, hurricanes or other environmental risks (Hasenauer and Kindermann, 2006).

Usually, tropical tree species present variable behavior under different conditions, even for the same species or same botanical families. Growth and mortality rates vary significantly between and within tree species, and also in relation to age, size, season, microclimatic conditions, tolerance to shade (Ferri, 1979) and monitoring time (Sheil and May, 1996). Therefore, due to the above reasons, it is recommended to predict growth of natural tropical forests in short periods of time (e.g. < 15 years), given that the growth of the species and site conditions can vary greatly and common explanatory variables used for forest modeling cannot capture this range of variation in longer periods of time.

The present study is an effort to model grow that individual level to support current and future research in the Atlantic Forest biome that require tree or stand level information, including forest management based on single trees and carbon sequestration potential, among others. It is based on available long term information corresponding to a series of permanent plots measured over a period of 14 years. Due to limitations on data we are not modeling the recruitment of the trees.

The objectives of this study are to: 1) identify important stand and tree level variables that help explaining the response on growth and mortality of trees; 2) construct models that predict individual diameter increment, height-diameter relationship and mortality; and 3) evaluate different statistical fitting methods for the construction of diameter increment models.

MATERIAL AND METHODS

The area of this study correspond to a 17.0 ha site located in Viçosa, Minas Gerais State, in the southeast region of Brazil (42°52'30" W; 20°46'10"S). The vegetation of the region is classified as semideciduous montana forest. Based on species composition and stand parameters this area is also classified as secondary succession (Veloso *et al*.,1991). According to Köppen climatic classification the local climate is of the type Cwb, with an average maximum and minimum temperature of 26°C and 14°C, respectively, with hot and rainy summers and cold and dry winters. The average annual rainfall is about 1,338 mm (Oliveira Junior and Dias, 2005). The local topography is rugged, with strong relief-wavy and mountainous with narrow valleys and moist. The altitude ranges from 600 to 970 m.a.s.l. Soils of the study area are predominantly Oxisol Alic, (at the top of the hills and slopes) and Red-Yellow Cambic (predominates in interraces).

In this study were used 10 sample plots covering different productivities, soils, slopes and exposures of the terrain. Each permanent plot had 1,000 m² (20x50m), established in 1994 and re-measured in years 1997, 2000, 2004 and 2008. Individual trees were marked for botanical identification in each plot. Diameter outside bark at 1.30m was measured for all trees larger than 5cm as well as total height and height to base crown (i.e. stem height). The measurements were taken on the same trees. Summary statistics of the raw data from these 10 plots is presented in Table 1.

The forest studied presents high biological diversity, with a total of 144 identified tree species; however, only 23 of these (i.e. 16.2%) represent more than 64% and 69% of the trees and basal area per hectare, respectively (see Table 2). In addition to representing a high percentage of basal area and number of trees, these 23 species are also the most predominant in other forests in the Atlantic Forest region (Oliveira *et al*., 2005) and; hence, represent those with greater biological interest.

Linear and Non-linear Models Approach:

Individual diameter and height increments and mortality are functions of several stand tree level components such as tree size, site productive capacity, stand density and competition between trees (Hasenauer, 2006; Bueno and Bevilacqua, 2010). Thus, in this study the follow conceptual model was considered to construct individual models: Y = f(*tree*, *site*, *stand*, *competition*). Here, Y corresponds to the response variables of periodic annual increment in diameter at the end of measurement period (PAI_d, cm year^{-1}); total height

(H_t, m); or probability of mortality (*P(M)*); *tree* refers to one or more tree level variables measured at the beginning of the measurement period including diameter at breast height (*dbh*, cm); total height (H_t, m); or stem height (H_f, m); *site* identifies site quality variable, here, the average height of dominant trees (H_d, m), considering the six taller trees per plot; *stand* identifies several stand level variables including mean and maximum diameter of the trees (D_{min} and D_{max}, cm); basal area (*BA*, m^2 ha^{-1}); or number of the trees per hectare (*TPH*, trees ha^{-1}); and finally *competition* identifies individual or stand variables that describe the level of competition for a given tree such as cumulative basal area of trees larger than subject tree (*BAL*, m^2 ha^{-1}); or the ratio of the subject tree *dbh* to the average tree diameter of the stand (*BAI*).

Because of high within-stand variability, modeling the height increment is generally more difficult and unreliable than diameter. So, some forest models at individual level are composed by a diameter increment function followed by a static diameter-height equation in which height of the trees is estimated as a function of *dbh* and one or more stand level variables (Weiskittel *et al*., 2011). In this study, this approach was followed by fitting the conceptual model to total height and not periodic height increment.

For the fitting process the above explanatory variables were considered in their original units or they were log-transformed. Several linear and nonlinear models were fitted for PAI_d and H_t using ordinary least squares (OLS) and iterative methods (NLS), respectively. Statistical analyses were performed using the package Statistica (Statsoft, 2005). Assumptions about linear regression models as normality, multicolinearity, autocorrelation and homoscedasticity were verified by the use of the Lilliefors test (L), variance inflation factor (VIF), Durbin-Watson test (DW) and White test (W), respectively (Gujarati, 2002). Variables that presented a VIF greater than 10 were dropped from the analysis, as suggest by O'Brien (2007) and only significant variables (i.e. $p< 0.05$) were kept in the final models.

The following goodness-of-fit statistics (on their original units) were obtained for each of the final selected models:

$$R^2 = 1 - \frac{\sum_{i=1}^{n}\left(Y_i - \hat{Y}_i\right)^2}{\sum_{i=1}^{n}\left(Y_i - \bar{Y}\right)^2}; \qquad R_{adj} = 1 - \frac{n-1}{n-p-1}\left(1 - R^2\right) \tag{1}$$

$$BIAS(\%) = \frac{100}{\bar{Y}} \times \frac{\sum_{i=1}^{n}(Y_i - \hat{Y}_i)}{n}; \qquad \text{RMSE}(\%) = \frac{100}{\bar{Y}} \times \sqrt{\frac{\sum_{i=1}^{n}\left(Y_i - \hat{Y}_i\right)^2}{n}} \tag{2 and 3}$$

where R^2 = empirical coefficient of determination or model efficiency (Crescente-Campo *et al*., 2010) on the original variable; R^2_{adj} is the empirical adjusted coefficient of determination; BIAS% is the relative bias; RMSE% is the percentage root means square error; *n* is the number of the observations; *p* is the number of the explanatory variables; $\bar{Y}$ is the mean of the dependent variable; Y_i is the i-th observed value and $\hat{Y}_i$ is the estimated i-th value of the dependent variable.

As the individual tree mortality is a binary process, i.e. only the values 0 (live) or 1 (dead) may occur during a given measurement, a logistic regression was fitted to predict P(M) (Monserud, 1976; Buchman et al., 1983; Hamilton, 1986; Monserud and Sterba, 1999; Vanclay, 1991) based on a logit link using maximum likelihood estimation as implemented in Statistica (Statsoft, 2005). The statistics log-likelihood value, $\chi 2$ test and Wald statistics were used to select significant tree and stand level explanatory variables ($p< 0.05$).

Linear Mixed Model Approach:

Due to the large number of different species and the different levels of information from each of these, also a Linear Mixed Model (LMM) approach including both fixed and random effects components was implemented in order to obtain a PAI_d model for each species. LMMs are flexible models that allow modeling dependent observations and heterogeneity of variances (Littell *et al*., 2006).

In this study, a random regression model was fitted to the best model obtained from the previous approach. Here, a random effect was incorporated for each of the regression terms, which fits random effect parameter deviations that are specific to each species. The significance of the variance (and covariance) components from the above model were evaluated using a likelihood ratio test and the selection of the final models was based on the Akaike (AIC) and Schwarz (BIC) criteria (Littell *et al*., 2006). All of these analyses were done using the statistical package SAS (SAS, 2002).

The final model for PAI_d based on LMM was later evaluated by calculating goodness-of-fit statistics: $\bar{R}^2$, BIAS% and RMSE%, as described earlier on their original units. Comparison between the previous approach and the LMM fits were based

on these statistics for diameter increment to select the best models.

Evaluation Models:

Since there was not a set of independent data to validate the selected models, a simulation process was performed to evaluate them better. As the trees mortality is a stochastic process, these simulations allowed to observe the accuracy of predictions at tree and stand levels in short periods of time, i.e., for each monitoring period (1994-1997, 1997-2000, 2000-2004 and 2004-2008).

For each tree in a given plot, the probability of mortality, *P(M)*, based on data at the beginning of the monitoring period, was calculated and an uniformly distributed random number, u, was generated. If *P(M)*< u then the tree was considered dead during the period, otherwise it was considered alive. Later, for each alive tree the PAI_d and H_t were predicted by the selected models resulting in the final *dbh* and *Ht* estimates at the end of the monitoring period. This process was repeated 500 times for each plot in each monitoring period resulting in maximum and minimum estimates and the average number of dead trees during each period as well as average estimates of *dbh* and *Ht* for each tree and basal area per hectare (BA) at the end of each period. At the end of the evaluation (simulation) process the accuracy of the predictions at tree and stand level for each monitoring period was verified through the goodness-of-fit statistics *BIAS%*, *RMSE%* together with graphical displays.

Results:

Considering the trees during the monitoring period (1994-2008) the mean PAI_d was 0.14 ± 0.01cm (CI; p = 0.95). It also was observed that most trees (94.7%) grew less than 0.5cm year^{-1},with a maximum value of 1.43 cm year^{-1} (see Figure 1a) observed for a tree of *Anadenanthera peregrina*. The mean periodic annual increment in height (PAI_h) was 0.22± 0.01 m (CI; p = 0.95), with a maximum increment of 3.10 m year^{-1} (see Figure 1b), observed for a tree of *Bathysa nicholsonii*. In this period, a total of 144 species were sampled, of which 95 (i.e. 66.9%) showed some level of mortality. The species *A. peregrina*, *Aparisthmium cordatum*, *B. nicholsonii*, *Casearia ulmifolia*, *Piptadenia gonoacantha* and *Siparuna arianeae*, which are intolerant or slightly shadow tolerant represents 40.8% of dead trees. The number of dead trees decreased with increasing diameter (see Figure 1c). The height-diameter distribution (see Figure 1d) tends to an asymptotic value of around 35.0 m and shows high variability for a given diameter value.

Fitted Models:

The final selected models from fitting linear and non-linear models are:

$$\ln(10\times PAI_d+10) = \beta_0+ \beta_1\times dbh+ \beta_2\times H_t+ \beta_3\times BAL +\varepsilon \quad (4)$$

$$H_t= \exp(\beta_0 + \beta_1\times dbh + \beta_2\times BAL + \beta_3\times H_d + \beta_4\times dbh^{-1}) + \varepsilon \quad (5)$$

$$P(M) = \frac{e^{(\beta_0+\beta_1\times dbh+\beta_2\times D_{MAX}+\beta_3\times H_d)}+\varepsilon}{1+e^{(\beta_0+\beta_1\times dbh+\beta_2\times D_{MAX}+\beta_3\times H_d)}+\varepsilon} \quad (6)$$

According statistical tests the best model selected to estimate PAI_d for all species did not violate assumptions about errors (DW= 1.65, p-value < 0.00001; W=203.96, p-value < 0.00001, L=0.20, p-value < 0.00001) but resulted in a model with poor fit statistics ($\overline{R}^2$ =8.35%; BIAS%=2.28; RMSE%= 192.16), although explanatory variables diameter at breast height (*dbh*), total height (H_t) and the competition index (*BAL*) were all highly significant (p <0.004) (see Table 3). Note that the response variable for this model was expressed in cm and an offset was added in order to improve its approximation of the residuals to a normal distribution.

In relation to height-diameter model, the results (see Table 3) indicate that H_t is dependent on *dbh*, inverse of *dbh* (1/*dbh*), competition between trees (*BAL*) and average height of dominant trees (H_d), where all the model parameters associated these variables are highly significant (p <0.00001). Also, their sign indicate that trees with larger *dbh* and in sites with larger average height of dominant trees values tend to result in taller trees. In contrast, trees under higher levels of competition result in shorter trees. The height-diameter model fitted very well to the data ($\overline{R}^2$ = 76.61%; BIAS% = 0.059; RMSE% = 22.06).

The most significant explanatory variables in the logistic model to predict *P(M)* during monitoring period were *dbh*, D_{max} and H_d. Here, the model explained a significant proportion of the variability (-2logL = 2,987.45, χ^2 = 36.67 with p<0.00001). The signs associated with the explanatory variables (see Table 3) indicate that trees with larger diameter have lower *P(M)*as well as trees that belong to sites with larger average height of dominant trees. Furthermore, the higher the upper limit of the distribution of diameters the higher the *P(M)*.

The model to be fitted by linear mixed model methodology for the response variable PAI_d was:

$$\ln(10\times PAI_d+10) = (\beta_0+a_i) + (\beta_1+b_i)\times(dbh\times H_t/100)+ \beta_2\times BAL +\varepsilon$$

where β_0, β_1, β_2 are fixed model parameters; a_i is the random intercept of the i-th specie, with $a_i \sim N(0, \sigma^2_a)$; b_i is the random slope for the covariate $dbh\times H_t$ of the i-th specie, with $b_i \sim N(0, \sigma^2_b)$, in addition, a

covariate, σ_{ab}, was included to model relations among random effects belonging to the same tree. Also, errors, ε, belonging to the same tree where assumed to be correlated based on an autoregressive order 1 error structure (AR(1)), defined by a temporal correlation ρ and error variance σ^2_ε.

More complex models were evaluated that considered a third random effect for the explanatory variable *BAL* and their respective correlations among other random effects; however, these models resulted in no significant improvements from the model present above.

The final fitted linear mixed model to estimate PAI_d resulted, in comparisons to the linear model, in a slightly better fit but with larger overall bias($\overline{R}^2$ = 11.92%; BIAS% = 9.30; RMSE% = 188.47). All explanatory variables were highly significant (p <0.0001) (see Table 3). Significant variance components were obtained for the intercept and the slope associated with the variable $dbh \times H_t$ and a temporal correlation of 0.331 was estimated by this model. In addition the residuals showed a good approximation to the normal distribution.

Based on the 23 predominant species (see Table 2), the fitted linear mixed model resulted in more precise estimates of PAI_d for most species in relation to the linear model (see Table 4). This is expected, as the LMM is allowing for estimation of specific species deviations from the overall model and also is considering the correlated nature of the data. However, still some relatively large values of BIAS% and RMSE% were found for some species.

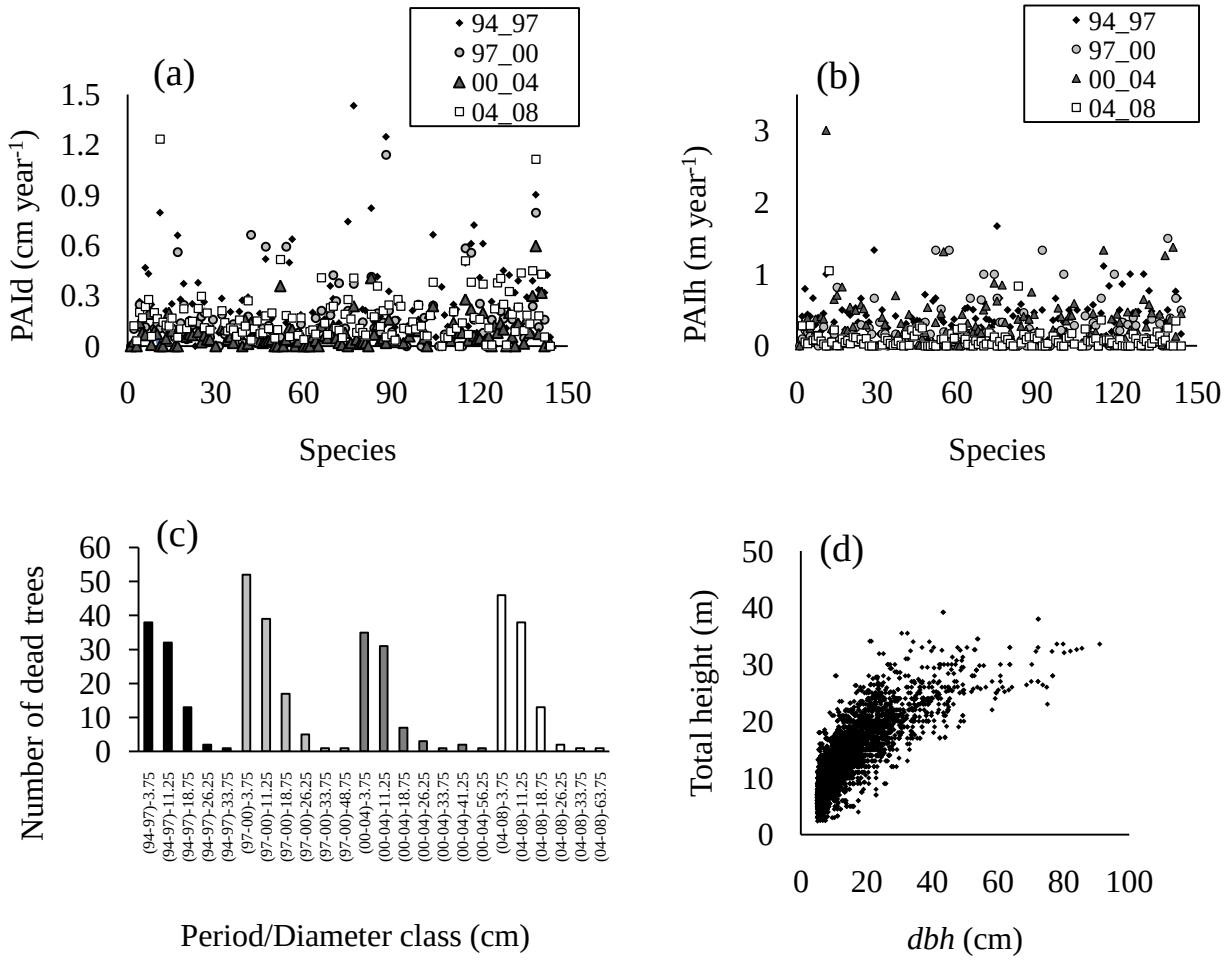

Fig. 1: Distribution of the periodic annual increments in diameter (a) and height (b) by species, number of dead trees (c) by diameter classes, during the monitoring period (1994(94);1997(97); 2000(00); 2004(04); 2008(08)) and diameter-height distribution (d).

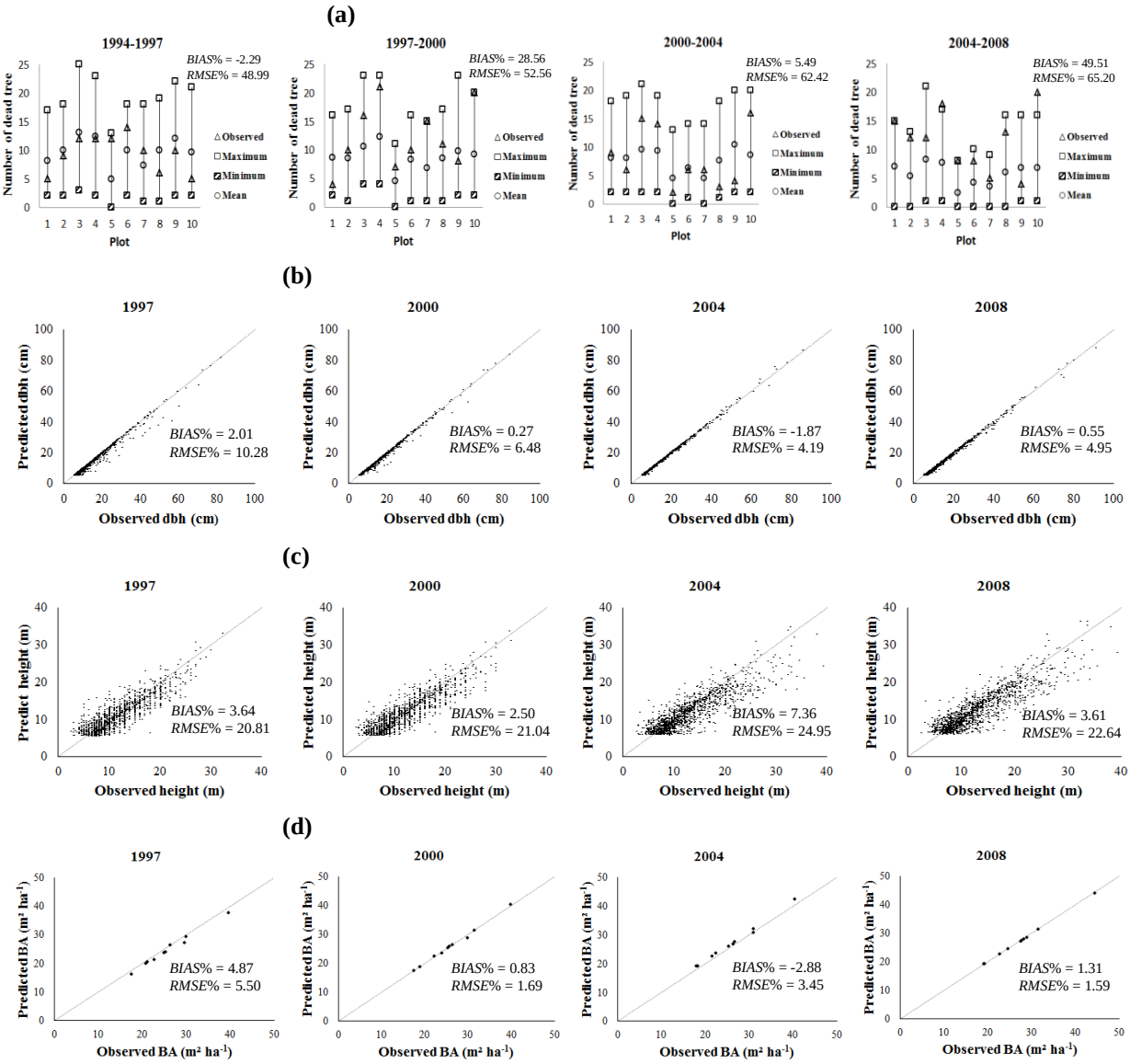

Fig. 2: Evaluation of the models to predict number of the dead trees (a), diameter and height of the trees (b and c), basal area per hectare (d) in a semideciduos Atlantic forest in Brazil.

Table 1: Summary statistics of 10 sample plots from Atlantic forests used in this study (1994-2008)

Variable	Range	Mean ± sd*
Basal area (*BA*, $m^2 ha^{-1}$)	16.98 – 44.61	26.50 ± 6.02
Number of trees (*TPH*, trees ha^{-1})	960 – 1,990	1,544 ± 235
Diameter at breast height (*dbh*, cm)	5.0 – 91.4	12.42 ± 9.11
Total tree height (H_t, m)	2.4 – 39.2	12.15 ± 5.54
Average height of dominant trees (H_d, m)	19.3 – 34.4	25.39 ± 3.62
Stem height (H_f, m)	2.0 – 24.0	7.72 ± 3.90
Periodic annual increment in diameter (PAI_d, cm $year^{-1}$)	0.0 – 1.43	0.142 ± 0.285
Periodic annual increment in height (PAI_h, m $year^{-1}$)	0.0 – 3.10	0.218 ± 0.372

* standard deviation; number of observations = 6.696

Table 2: Number of sampled trees and percentage of basal area (from total) on predominant species from the 10 permanent plots. Percentages are presented within parenthesis

Species	Number of trees					% Basal area				
	1994	1997	2000	2004	2008	1994	1997	2000	2004	2008
Allophylus edulis	13	13	13	14	15	0.87	0,86	0.89	0.94	1.00
Anadenanthera peregrina	54	52	45	46	41	18.19	18.68	18.85	19.88	18.87
Aparisthmium cordatum	82	75	62	57	63	1.78	1.48	1.12	1.05	1.21
Apuleialei ocarpa	46	45	45	43	47	4.83	4.64	4.84	5.01	5.17
Bathysa nicholsonii	113	126	126	125	125	3.64	4.09	4.41	4.56	4.90
Casearia arborea	22	22	22	20	19	2.31	2.44	2.62	2.48	2.56
Casearia ulmifolia	71	69	67	65	59	5.36	5.47	5.57	5.69	5.49
Cecropia hololeuca	8	8	8	8	8	2.74	2.75	2.79	2.84	2.85
Inga alba	8	5	2	2	2	2.14	1.48	1.16	1.20	1.16
Jacaranda macrantha	42	42	41	41	36	1.43	1.39	1.39	1.40	1.23
Lacistema pubescens	31	32	31	31	30	1.21	1.24	1.20	1.19	1.12
Mabea fistullifera	23	26	21	20	23	1.15	1.15	0.96	0.94	0.91
Machaerium floridum	19	19	19	17	15	1.69	1.68	1.63	1.65	1.51
Myrcia formosiana	34	32	30	29	28	1.30	1.25	1.27	1.29	1.25
Newtonia contorta	41	38	39	40	39	6.59	6.92	7.28	7.67	8.54
Ocotea odorifera	24	26	26	28	32	1.33	1.49	1.60	1.79	2.00
Piptadenia gonoacantha	29	25	22	15	18	2.47	2.27	2.19	1.46	1.59
Platypodium elegans	17	16	14	13	14	2.77	2.61	2.49	2.50	2.47
Prunus sellowii	20	21	21	21	19	0.82	0.84	0.89	0.91	0.81
Rollinia sylvatica	35	33	29	28	26	2.38	2.25	2.14	2.21	2.08
Siparuna arianeae	126	149	157	170	186	1.83	2.07	2.16	2.28	2.42
Tapirira peckoltiana	12	12	11	10	9	2.17	2.40	1.69	0.67	0.66
Trichilia catigua	9	12	15	17	18	0.20	0.27	0.32	0.38	0.45
Subtotal	879 (64.25)	898 (65.17)	866 (65.26)	860 (66.05)	872 (66.01)	69.19	69.73	69.45	69.98	70.27
Other Species	489 (35.75)	480 (34.83)	461 (34.74)	442 (33.95)	449 (33.99)	30.81	30.27	30.55	30.02	29.73
Total	1,368	1,378	1,327	1,302	1,321	100	100	100	100	100

Table 3: Estimates of the parameters, standard error (SE) and p-values associate to models for PAI_d, H_t and *P(M)* in a semideciduous Atlantic forest in Brazil

Dependent variable	Explanatory variables	Parameters estimates	SE	p-value
	Linear and Non-linear model approach			
PAI_d	Intercept	4.610092	0.001775	<0.00001
	dbh (cm)	0.000482	0.000073	<0.00001
	H_t (m)	0.000562	0.000116	<0.00001
	BAL ($m^2 ha^{-1}$)	-0.000160	0.000055	0.00384
H_t	Intercept	2.668428	0.018925	<0.00001
	dbh (cm)	0.005101	0.000303	<0.00001
	BAL ($m^2 ha^{-1}$)	-0.004316	0.000464	<0.00001
	H_d (m)	0.018295	0.000803	<0.00001
	$1/_{dbh}$ (m)	-6.486452	0.090776	<0.00001
P(M)	Intercept	-0.870221	0.404289	0.03143
	dbh (cm)	-0.022521	0.007677	0.00333
	D_{max} (m)	0.011144	0.004005	0.00537
	H_d(m)	-0.096936	0.020113	<0.00001
	Linear Mixed Model Approach			
PAI_d (Fixed effect)	Intercept	2.44600	0.0124600	<0.0001
	dbh×H_t/100 (cm.m)	0.01414	0.0026950	<0.0001
	BAL ($m^2 ha^{-1}$)	-0.00215	0.0000459	<0.0001
Variance component	σ^2_a	0.000918	0.000353	0.0047
	σ^2_b	0.000147	0.000063	0.0094
	ρ	0.331200	0.016110	<0.0001
	σ^2_ε	0.025521	0.000541	<0.0001
	σ^2_{ab}	0.000000	-	-

Table 4: Statistics for 23 predominant species considering fitted linear mixed model and linear model to predicted PAI_d in a semideciduos Atlantic forest

Species	Linear Mixed Model				Linear Model	
	$\beta_0 + a_i$	$\beta_1 + b_i$	BIAS%	RMSE%	BIAS%	RMSE%
Trichilia catigua	2.50327	0.01818	24.34	61.36	55.78	81.21
Ocotea odorifera	2.49508	0.02529	13.07	81.14	44.74	91.52
Allophylus edulis	2.44167	0.01093	-2.32	108.44	-27.31	114.61
Lacistema pubescens	2.45996	0.00797	4.40	113.02	7.03	117.40
Aparisthmium cordatum	2.44929	0.00829	5.99	130.77	15.26	132.86
Casearia arborea	2.47719	0.01320	13.46	131.44	14.95	132.68
Apuleialei ocarpa	2.39629	0.01919	-4.30	136.09	-62.34	149.79
Prunus sellowii	2.44177	0.00825	5.42	138.00	-7.88	143.30
Siparuna arianeae	2.42311	0.00890	-2.52	143.72	-12.49	143.07
Platypodium elegans	2.42009	0.00929	-4.35	156.87	-65.90	170.82
Piptadenia gonoacantha	2.42326	0.01344	-3.84	157.81	-48.08	163.15
Rollinia sylvatica	2.45235	0.00502	8.88	160.66	-18.32	165.77
Newtonia contorta	2.43157	0.03358	8.19	163.21	30.44	175.32
Bathysa nicholsonii	2.44151	0.02010	6.29	180.13	12.58	178.86
Jacaranda macrantha	2.41332	0.00297	-10.44	180.16	-90.34	211.99
Cecropia hololeuca	2.44950	0.00668	13.91	197.30	-43.48	204.55
Anadenanthera peregrina	2.47630	0.01077	22.51	200.02	14.03	196.83
Machaerium floridum	2.42553	0.01415	2.27	208.39	-37.24	208.53
Myrcia formosiana	2.42699	0.01947	5.97	209.52	-8.12	207.78
Mabea fistullifera	2.42886	0.00175	2.67	213.72	-52.09	226.44
Casearia ulmifolia	2.44693	0.00910	11.41	219.69	-12.97	218.79
Tapirira peckoltiana	2.45974	0.02352	20.72	242.77	33.08	244.15
Inga alba	2.44866	0.00773	28.42	275.68	11.15	272.00

Evaluation Models:

Most of the observed number of dead trees (observed) in the monitoring periods are between the minimum and maximum estimates predicted by the evaluation process (simulation) and by equation 6 (see Figure 2a), showing the potential of this system to predict tree mortality. Except the first monitoring period (1994-1997) there was tendency of underestimation of the number of dead trees, according to BIAS% and RMSE% estimates. Regarding predictions of *dbh*, *Ht* and *BA* by equations 7 and 5, estimates of goodness-of-fit statistics and graphical displays indicate a slight tendency of underestimation of these parameters (see Figures 2b, 2c and 2d).

Discussion:

In terms of the mean PAId this study showed similar results to values reported in other Brazilian biome (the Amazon forest), corresponding to an observed diameter increment equal to 0.16 cm year^{-1} in the Jacaranda project, near at Manaus city, capital of Amazon State (Silva *et al*., 2002). The observed high percentage of mortality of shade intolerant species and concentrated in smaller diameter classes are a tendency in tropical forests (Denslow, 1987; Pulz,1998).

The selected models in the linear and non-linear model approach and linear mixed model approach do not fitted well to the observed data. Normally individual-tree-models are incapable of predicting the growth of a specific individual tree with any reliability due to low R^2 values (Bueno and Bevilacqua, 2010). Phillips *et al*. (2004) have fitted similar equations as fitted in the first approach to predict the PAI_d for groups of species in the Amazon and found poor fit statistics (coefficients of determination between 3.3% and 18.3%), using *dbh* and a distance independent competition index as explanatory variables.

The signs associated to the parameters in the selected models to predict PAI_d are biologically reasonable, i.e., trees with larger diameters and heights tend to grow more (in absolute terms) and under increased levels of competition trees tend to grow less. However, as the relationship between the diameter of the trees and their increment in diameter is represented by a curve with a maximum point (Vanclay, 1994) the selected model to predict PAI_d will provide reliable estimates of growth over a limited range of diameters given that trees with larger diameters always grow more.

The wide dispersion of the heights of trees in tropical forests as observed in this study can results in equations with low explanatory power, introducing estimation error higher than the periodic increments (Vanclay, 1994; Hasenauer and Monserud, 1997). For example, Batista *et al*. (2001) found coefficients of determination between 28 and 36%, evaluating several height-diameter models in a tropical forest in the State of Maranhão, Brazil, where *dbh* was the only independent variable.

The inverse diameter in the select height-diameter model behaves similarly when is included in the mortality model (Chatziphilippidis and Spyroglou, 2006), where it describes well the rapid decline from high mortality for small trees to a more gradual decline in mortality for large diameter trees. In this case, the parameter associated with this variable describes the rate of decrease of height with increased diameter of trees, tending tree height an asymptotic value (see figure 1d).

To increase the precision of the estimates obtained in this study random effects were included

in the periodic annual diameter increment within the framework of linear mixed models. Although this methodology has provided a fit slightly better important gains in the precision of the estimates was observed for predominant species and, consequently, contributed to more accurate estimates of basal area per hectare in the evaluation process. In addition, it was possible to estimate individual relationship even for those species that have limited number of observations.

In this study we predicted the probability of mortality for all species as a single group. Prediction for each species is difficult due to large number of species present and to the limited amount of information that such a binary trait provides. However, to increase the precision of these estimates it is possible to consider only predominant species together with a weighting variable. According to Hasenauer (2006) one of difficulties in calibrating mortality models is that mortality is a rare event and can be greatly affected by external aspects such as drought stress or disease, making the mortality modeling process difficult and expensive due to large amount of data required to reach reasonable levels of precision. Thus, the individual tree mortality predictions may be considered as one the most challenging tasks within tree growth modeling, although imprecise predictions may not result in bad estimates of stand level variables such as basal area, as showed in this study.

In the evaluation process of the selected models it was observed that the equation to predict PAI_d (Eq.7) resulted in accurate estimates of *dbh* at the end of each monitoring period (see Figure 2b), even not fitting well to the observed data (low R^2). As the trees grow little in diameter annually (0.14 ± 0.01 cm) and the evaluation period was short, the low precision of the estimates of PAI_d had no significant influence on the final estimates of *dbh* at the end of each period.

To improve estimates an alternative methodology to the one used here is to group data (cohort models) according some characteristic of the population, such as, species, size, vigor (e.g. crown status) and commercial characteristics (e.g. wood value) to later be used on forest management models (Vanclay, 1994). However, the use of any cohort model is restricted to the fitted data set used, since typically hundreds of species of trees exist in tropical forests and several alternative groups can be formed, this alternative is of limited use.

In order to obtain more consistent increment and mortality predictions, any growth model at individual tree level based on natural forest must include the ingrowth of trees in the smallest diameter class (Hasenauer, 2006). Future work is planned for this aspect based on available data for Atlantic forest. Therefore, some underestimations of the stand level variables (e.g. basal area) are expected from the implementation of the models presented here. However, this bias is expected to be small because the annual ingrowth represents approximately 1% of the number of trees, and affects small diameters.

Ingrowth can be modeled in a static way, which assumes an expected value of the number of trees that will join overtime, or dynamically, where the number of trees is estimated as a function of stand density, composition, mean diameter and other parameters (Vanclay, 1989). Thus, as the growth model at individual tree level consists of a system of equations, more accurate estimates for forest can predict better the ingrowth of trees. Also, as indicated earlier, for realistic ingrowth modeling, the sampling design should cover the range of forest conditions as well as capture the exact time of ingrowth of the trees (Leak and Graber, 1976). This second condition is often difficult to achieve as re-measurements inventories are often conducted in large time intervals (e.g. 5 years) yielding to larger measurement errors (Hasenauer and Monserud, 1997).

Conclusions:

The relatively small sample size and relatively short period of monitoring limits the generalization of results obtained in this study but it was possible to identify several explanatory variables assist on the prediction of periodic annual increment in diameter (PAI_d), height-diameter relationship and probability of mortality. The PAI_d model was fitted using traditional methodology, but the inclusion of random intercepts and slopes within the framework of linear mixed models resulted in important gains in precision for most of the predominant species evaluated. The height-diameter model fitted well to the observed data by the use nonlinear regression methods and the fitting of a logistic model to predict probability of mortality provided with moderate precision for prediction of number of dead trees for most periods; however, this did not affected importantly the estimation of basal area per hectare for any given period.

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