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HEIGHT-DIAMETER RELATIONSHIPS FOR *Araucaria angustifolia* (BERTOL.) KUNTZE IN SOUTHERN BRAZIL

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ABSTRACT: Height-diameter relationships are used in order to make forest inventories less expensive and to assess growth and yield. This study aimed to develop height-diameter models for individual trees of *Araucaria angustifolia* (Bertol.) Kuntze for different locations and growth conditions in Southern Brazil. Our data include locations of at least one third of this species natural geographical distribution. We used Michailoff's model, and compared height-diameter tendency through analytical methods. The model showed good overall precision and accuracy. Trees growing in forest conditions had a higher asymptotic height, and reached it at smaller diameters than open-grown trees. Different regions had contrasting height-diameter tendency indicating site potential, especially for natural forests. Individual tree asymptotic height was correlated with site altitude and mean annual precipitation. This study represents a source of parameters for height-diameter relationships in a large geographical span, for a species with high cultural and timber value in Southern Brazil.

RELAÇÃO ALTURA-DIÂMETRO PARA *Araucaria angustifolia* (BERTOL.) KUNTZE NO SUL DO BRASIL

RESUMO: A relação entre a altura-diâmetro são usualmente empregadas com intuito de obter inventários florestais menos custosos e para avaliar o crescimento e a produção. Este estudo teve como objetivo desenvolver modelos de altura-diâmetro para árvores individuais de *Araucaria angustifolia* (Bertol.) Kuntze para diferentes locais e condições de crescimento no Sul do Brasil. Os dados incluem localização de pelo menos um terço da distribuição geográfica natural da espécie. Foi utilizado o modelo de Michailoff e a comparação das tendências de altura-diâmetro por meio de métodos analíticos. O modelo mostrou de forma geral boa precisão e acurácia. Árvores que crescem em condições de floresta tem uma altura maior assintótica, alcançando em diâmetros menores do que as árvores crescendo livre de competição. Diferentes regiões tem contrastantes tendência altura-diâmetro indicando potencial local, especialmente para florestas naturais. A assíntota do modelo de altura das árvores apresentou correlação com a altitude local e precipitação média anual. Este estudo representa uma fonte de parâmetros das relações altura-diâmetro em uma ampla extensão geográfica, para uma espécie com alto valor cultural e potencial madeireiro no Sul do Brasil.

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INTRODUCTION

Individual tree height is one of the most important variables to be obtained in a forest inventory. It has several ecological implications and is related to succession and dynamics (CLARK; CLARK, 2001) of natural forests. Individual tree height affects management decisions, being essential to determine individual tree volume (JAYARAMAN; LAPPI, 2001) and, consequently, stand volume (HUANG et al. 2000). It plays a major role in density management diagrams (CASTAÑO-SANTAMARÍA et al., 2013), linking mean basal area and total volume. And, most importantly, it is used to develop site index, which allows forest managers to rank different forest locations into productivity classes (VANCLAY, 1994; JAYARAMAN; LAPPI, 2001). There is a fairly high correlation between forest height and forest biomass (NOGUEIRA et al., 2008), and thus carbon. When combined with the advent of digital elevation models, this correlation allow to obtain stand height, and to estimate above-ground carbon stocks (SIMARD et al., 2006) in a global scale.

However, obtaining tree height for inventories and validation data is time consuming and therefore costly (LEI et al., 2009). Besides, the need to use distances and angles (CRECENTE-CAMPO et al., 2010) makes measuring individual trees much prone error, especially in forests with dense understories. A common solution used in forest inventories is to measure a subsample (DIAMANTOPOULOU; ÖZÇELİK, 2012) or no individual tree heights at all (ADAME et al., 2008), and use height-diameter (h - d) relationship models to estimate heights (TEWARI; KISHAN KUMAR, 2002; SHARMA; PARTON, 2007; BUDHATHOKI et al., 2008). The h - d models are usually asymptotic equations of growth models that explain height variation through diameter measurements. Therefore, nonlinear estimation is inherently better for developing h - d models (CLUTTER et al., 1983). Besides, models should be parsimonious and their parameters biologically interpretable. Moreover, the data used to develop h - d models should cover a large spectrum of ontogenetic individual tree development, once sampling large trees only would mean a model with no realistic behavior or inflexion points (ADAME et al., 2008), and a dataset with small trees only would represent no actual knowledge of the maximum tree height potential (ZHANG, 1997).

The height-diameter curves based on diameter only cannot be used for all forest conditions and regions. The development of h - d models for each ecoregion is necessary to improve the accuracy of prediction

(CALAMA; MONTERO, 2004; ADAME et al., 2008). Furthermore, these models should be species-specific, since each species has its own *efficiency vs safety* growth strategy (SPERRY et al., 2008). The Ombrophilous Mixed Forest (OMF) is a forest formation in high altitudes of Southern Brazil (ZANINI; GANADE, 2005; SOUZA et al., 2008), which is characterized by the high dominance of the coniferous tree *Araucaria angustifolia* (Bertol.) Kuntze. This forest extends between latitudes 18° and 30° S. However, due to the high quality and value of timber of *A. angustifolia*, this extension has been reduced to 12% of the natural area (RIBEIRO et al., 2009).

Given the economic, social and ecological importance of *A. angustifolia* it is surprising that the developed height-diameter relationships developed for this species are limited to single stands. To overcome this lack of knowledge, this study aimed to develop a height-diameter model for *A. angustifolia* for different sites and habitats, and to test whether these sites could be grouped in the ecoregions regarding the behavior of this species.

MATERIAL AND METHODS

Data

A total of 2,108 trees of *A. angustifolia* had their d (diâmetro a 1,30 m do solo) and total heights (h) measured. These data pairs were obtained from seven different locations in Southern Brazil (Table 1), more specifically in the states of Rio Grande do Sul (RS) and Santa Catarina (SC). These data cover most of the southern part of the natural distribution of *A. angustifolia*. Even though it may seem that it is a small fraction of the latitude span where this species occurs, it should cover at least one third of the total area of occurrence, once this species naturally exists only in areas with relatively high altitude.

TABLE 1 Location and climate characteristics of the locations in which height-diameter data was obtained for *A. angustifolia*

Municipality	State	Code	Latitude	Longitude	Altitude	Mean Annual Temperature	Mean Annual precipitation
Chapecó	SC	CH	-27°05'	-52°36'	582	18.1	2,069.4
Três Barras	SC	TB	-26°06'	-50°18'	799	17.4	1,564.1
Canoinhas	SC	CN	-26°10'	-50°22'	831	17.2	1,607.4
Lages	SC	LG	-27°48'	-50°19'	987	15.2	1,684.7
Caçador	SC	CA	-26°46'	-50°59'	1,066	15.8	1,736.4
Nova Prata	RS	NP	-28°46'	-51°36'	661	16.5	1,980.5
Canela	RS	CL	-29°22'	-50°49'	675	15.9	2,033.0
São Francisco de Paula	RS	SF	-29°26'	-50°35'	854	15.0	2,016.4

In addition to different locations, data were obtained from different forest types and growing conditions. In even-aged plantation forests, mean basal area trees were measured in a variety of different tree ages, whereas in uneven-aged natural forests, trees of the whole diameter range were measured in each location. Furthermore, open-grown trees (OGTs), were obtained from agricultural land or cattle grazing fields. Total data showed a large range of diameters and heights for different conditions and locations (Table 2).

TABLE 2 Summary statistics of diameter at breast height (d) and tree total height (h) for *A. angustifolia* in different locations in southern Brazil.

Location	Condition	d (cm)					h (m)				
		N	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD	
CN	OGT	66	36.4	14.5	66.8	12.52	15.6	8.3	23.3	3.66	
LG		115	41.6	18.0	68.1	10.35	12.5	7.3	18.0	2.62	
Total		181	39.7	14.5	68.1	11.43	13.7	7.3	23.3	3.37	
LG	UANF	555	40.7	9.9	85.8	14.66	17.1	7.2	24.9	3.35	
NP		66	46.8	10.1	73.9	14.9	20.4	12.3	26.3	2.69	
SF		964	40.7	9.7	97.5	21.13	19.0	7.7	29.0	3.85	
Total		1,585	40.9	9.7	97.5	18.9	18.4	7.2	29.0	3.76	
TB	EAPF	61	25.3	16.0	35.0	5.63	17.3	13.9	21.0	2.27	
CA		148	23.8	10.2	41.4	7.98	14.7	7.8	20.3	2.59	
SF		60	25.4	8.5	40.0	8.07	15.5	6.8	22.3	3.62	
CL		43	30.0	8.5	53.0	12.42	15.7	8.0	23.4	3.73	
CH		30	26.6	17.3	45.8	6.62	17.6	13.5	20.5	1.89	
Total		342	25.4	8.5	53.0	8.42	15.7	6.8	23.4	3.04	

Where: N = number of trees measured; SD = standard deviation.; OGT - Open-grown tree; UANF - Uneven-aged-natural forest; EAPF- Even-aged plantation forest.

Model adjusted

Michailoff's model [1] was used to describe the h - d relationship of *A. angustifolia* trees. This model was selected because it has explained data tendencies well in this region (COSTA et al., 2014) and elsewhere (PAULO; TOMÉ, 2009; PRETZSCH, 2009). Furthermore, this model is highly parsimonious as it has only two coefficients. In biological terms, α means the asymptotically maximum height, and $\beta/2$ corresponds to the inflexion point, in which the lower the coefficient, the smaller the diameters in which the asymptote is reached. Also, the model has a fixed intercept of 1.3, which means that height is 1.3 when diameter equals zero, so this model could be characterized as constrained (NEWTON; AMPONSAH, 2007). Where: h is total tree height (m); d is tree diameter at breast height (cm); α and β are parameters estimated.

$$h = 1.3 + \alpha \exp\left(-\frac{\beta}{d}\right) \quad [1]$$

In order to compare whether the h - d tendencies for the different geographical regions (Table 2) were similar or distinct, we used two methods that are commonly

referred to in the literature (GONZÁLEZ et al., 2005; ADAME et al., 2008; CASTAÑO-SANTAMARÍA et al., 2013): the nonlinear extra sum of squares [2] (BATES; WATTS, 1988; KUTNER et al., 2004) and Lakkis-Jones test [3] (KHATTREE; NAIK, 2000). Where: is the sum square error of the reduced model; is the sum square error of the full model; is the degrees of freedom for the reduced model; and is the degrees of freedom for the full model; follows a distribution with degrees of freedom and F value follows F-distribution. F-test was normally considered significant if the P-value for the test is less than 0.05.

$$F = \frac{(SSE_R - SSE_F)/(Df_R - Df_F)}{SSE_F/Df_F} \quad [2]$$

$$L = (SSE_F/SSE_R)^{n/2} \quad [3]$$

Both comparison methods require that a full model and reduced models be fit to the data. In order to facilitate this process, an indicator (Dummy - D_i) variable approach was used [4] (HUANG et al., 2000). Where: h is total tree height (m); d is tree diameter at breast height (cm); α and β are parameters estimated; D_i = indicator (Dummy - D_i).

$$h = 1.3 + (\alpha + \alpha_1 D_i) \cdot \exp\left(-\frac{\beta + \beta_1 D_i}{d}\right) \quad [4]$$

Model assessment

As model developers, we expect to provide as much information about models errors (ZHANG, 1997; NEWTON; AMPONSAH, 2007) as possible, making a distinction between model accuracy (mean prediction error) and precision (model standard error) (VANCLAY et al., 1997), especially for model's end users (BRAND; HOLDAWAY, 1983). In order to do so, we provide the determination coefficient (R^2) [5] and root mean standard error (RMSE) [6] as precision measures. Where: is the observed value for i^{th} observation; is the predicted value for i^{th} observation; is mean of the; is the number of observations in the dataset; is the number of estimated parameters.

$$R^2 = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad [5]$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{n - k}} \quad [6]$$

In order to assess model consistency throughout the whole data range, we plotted observed residuals against diameter. We tested Pearson's correlations between environmental variables of each location and adjusted asymptote and inflexion points of the $h-d$ tendencies, considering values weak correlation ($\sigma < |0.3|$), moderate ($|0.3| < \sigma < |0.7|$) and strong ($\sigma > |0.7|$). The Statistical Analysis System (SAS Institute 2002) was used in the analysis, and PROC NLIN procedure and Marquardt method were used to estimate the model parameters and statistics.

RESULTS

Coefficients varied greatly among tree location and conditions (Table 3). As the asymptotically maximum estimated height varied approximated from 20 to 26 m, the inflexion point measured by the β coefficient seems to be the most striking difference among locations and, especially, conditions.

TABLE 3 Estimated parameters, precision and accuracy of the height-diameter relationship for *A. angustifolia* in different locations and by condition of trees in Southern Brazil

Location	Condition	α	β	R^2	RMSE
CN	OGT	25.9889	19.9290	0.7382	1.8881
LG		22.6403	27.9849	0.5611	1.7426
Group		20.6769	19.1412	0.3394	2.7484
LG	UANF	23.0727	13.6800	0.5409	2.2701
NP		23.7098	8.7709	0.5433	1.8338
SF		23.9607	9.4302	0.6931	2.1315
Group	EAPF	23.1311	10.0152	0.5559	2.5100
TB		24.8262	10.6980	0.4987	1.6223
CA		21.2773	9.9863	0.7193	1.3762
SF	EAPF	23.8434	12.1111	0.6123	2.2727
CL		23.4958	12.5915	0.8181	1.6123
CH		25.1232	11.0712	0.7870	0.8886
Group		23.1764	11.0563	0.6561	1.7863

OGT - Open-grown tree; UANF - Uneven-aged-natural forest; EAPF- Even-aged plantation forest.

However, the model showed good behavior throughout the diameter range (Figure 1). Open-grown trees reach the same diameter at a much younger age, thus, showing smaller heights for that diameter. Trees from natural forests reach maximum expected heights at slightly smaller diameters than trees from plantations. Along with the mean tendency, overall model precision and accuracy varied among locations and conditions. The models developed for trees of even-aged plantations forests have a better precision and accuracy than models developed for trees in uneven-aged natural forests or in open-grown trees conditions.

Even though we can deduce tendencies from the estimated mean coefficients, comparisons based

on these values are blurred by model accuracy and precision. Therefore, analytical methods such as Lakkis-Jones and the nonlinear extra sum of squares allow us to draw significance lines of how different locations and tree-growing conditions could be pooled in one group, or segregated (Table 4). The $h-d$ average tendency was not different between trees in even-aged plantations and uneven-aged natural forest conditions, but both groups were distinct from open-grown trees. Moreover, groups of different locations can be created.

DISCUSSION

The model showed overall good behavior, explaining from 30 up to 80% of total height variation, with standard errors from 1.3 to 2.7 m. Models for individual locations had high accuracy. These results are in accordance with the values observed in the literature in terms of accuracy and precision (HUANG et al., 2000; COLBERT et al., 2002; PENG et al., 2004; ADAME et al., 2008; OUZENNOU et al., 2008; LEI et al., 2009; CRECENTE-CAMPO et al., 2010).

We believe that other $h-d$ models developed or to be developed for *A. angustifolia* may have better statistics when using a smaller set of data, or a narrower geographical range, but the developed models in this manuscript could easily be used for the many applications already mentioned. Moreover, it is unlikely that another model would have the same parsimonious characteristics and biological interpretation at the same time. Although interpolation could be used to obtain equations that suit locations away from the geographical points sampled in this study, care should be taken when using the models outside the diameter range or too far from the sampling locations.

It is known in inventories that increasing sample size should reduce the errors in estimates (KANGAS; MALTAMO, 2006). However, we have found no such trend in our data, therefore, the number of pairs of diameters and heights obtained in each location should be considered sufficient. Our subsample sizes varied from 30 to over 964 pairs of observed diameters and heights, therefore, inventories to determine $h-d$ relationships, in broad geographical areas, do not need such intense sub-sampling. Resources would be better spent in a small (~ 30 pairs of data) number of trees in a heavier sampling grid (more sample locations) over the region under study. Testing smaller data subsamples could provide a maximum efficiency point between number of data pairs and number of subsample locations (CALAMA; MONTERO, 2004). However, our data lack such characteristics.

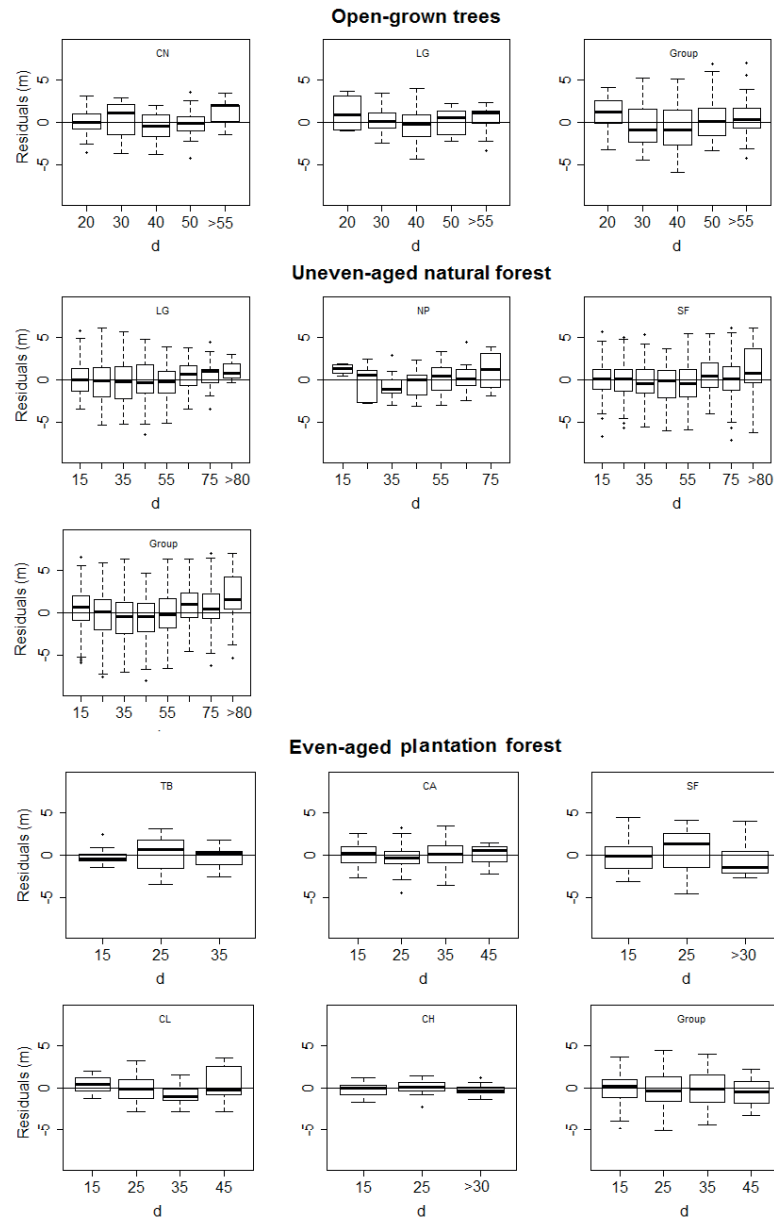


FIGURE 1 Box-plots of residuals of height-diameter relationship for *A. angustifolia* in southern Brazil, for different tree growing conditions.

Large differences could be observed between the inflexion points of trees growing in forest conditions and the open-growing trees, as trees from natural forests and plantations had much lower inflexion points. It is in accordance with the thinning theory (and must happen in liberation as well), in which after such operation, trees grow in diameter in detriment of height (CRECENTE-CAMPO et al., 2010). Trees in high light environment tend to expand their crowns and leaf area index (STERCK; BONGERS, 2001) to absorb the available energy, thus, they need more water-conducting structures, growing more in diameter than in height. This growth offset must still be inside the

range of the species efficiency vs safety growth strategy. The larger self-shading of leaves that is observed in larger trees is probably due to the need to adapt to an environment with more light and water stress (RYAN et al., 2006; DUURSMA et al., 2010). Another effect in the inflexion point could be tree age, as older trees should have a lower inflexion point (ADAME et al., 2008). However, this variable cannot be obtained in natural forests, unless full increment cores are taken from the trees, a situation that could be challenging given the large diameters of our trees. Furthermore, age is, most of the times, substituted with tree dimension in natural forest growth simulators.

TABLE 4 Statistics results of the pairwise comparisons by nonlinear extra sum of squares (F-value) and Lakkis and Jones (L-value) used to assess regional differences between reduce and full models for *A. angustifolia* in Southern Brazil.

Pairwise comparisons	Full model		Reduced model		N	F-value	L-value
	DfF	SSEF	DfR	SSER			
Open-grown tree							
CN - LG	177	571.3	179	1352.1	181	121.0*	155.9*
Uneven-aged natural forest							
LG - NP	617	3065.1	619	3459.6	621	39.7*	75.2*
LG - SF	1515	7220.7	1517	9686.8	1519	258.7*	446.3*
NP - SF	1026	4586.0	1028	4587.4	1030	0.2	0.3
Even-aged plantation forest							
TB-CA	205	431.8	207	583.1	209	35.9*	62.8*
TB-CH	87	177.4	89	177.5	91	0.0	0.1
TB-SF	117	454.9	119	521.1	121	8.5*	16.4*
TB-CL	100	261.9	102	354.1	104	17.6*	31.4*
CA-CH	174	298.6	176	387.7	178	26.0*	46.5*
CA-SF	204	576.1	206	590.7	208	2.6	5.2
CA-CL	187	383.1	189	393.7	191	2.6	5.2
CH-SF	86	321.7	88	362.4	90	5.4	10.7*
CH-CL	69	128.7	71	192.1	73	17.0*	29.2*
SF-CL	99	406.2	101	411.7	103	0.7	1.4
Open-grown tree - Uneven-aged natural forest	1762	11325.1	1764	15802.7	1766	348.3*	588.4*
Open-grown tree - Even-aged plantation forest	519	2437.1	521	4501.4	523	219.8*	320.9*
Even-aged plantation forest - Uneven-aged natural forest	1923	11057.9	1925	11152.8	1927	8.3	16.5

* Significant probability ($\alpha=0.05$).

The asymptotic height development was not different for trees from both even-aged plantations and uneven-aged natural forests. It contradicts the fact that damage can play a role in height growth in natural forests (CLARK; CLARK, 2001). This happens because the height growth strategy of *A. angustifolia* (monopodial growth) is different from most trees in tropical forests (HALLÉ et al., 1978). Likewise, in the inflexion point, open-grown trees had a distinct *h-d* behavior from forest trees regarding the asymptotic height development. An oversimplistic explanation would be that lack of competition inhibits height development. However, we believe that other environmental factors play a major role in this situation as well. Forest conditions provide protection for the soil from light, heat, wind (YORK et al., 2003) and, therefore, an environment with more water availability, which is a major factor to determine potential height development (YORK et al., 2003; KOCH et al., 2004).

Individual tree and stand development are intimately linked (ADAME et al., 2008). Eichhorn's rule (SKOVSGAARD; VANCLAY, 2008) states that total volume production in a given stand height should be the same for one species in all sites, given that densities are not extreme (between ~500 and ~2500 trees.ha⁻¹). Therefore, the *h-d*

tendencies observed in this study could indicate forest productivity in different locations and conditions (HUANG; TITUS, 1993). However, many other factors influence forest yield such as age, management and tree genetics. Thus, care should be taken when using *h-d* relationship in relation to productivity.

The development of ecoregion models is needed for fine tuning management and ecosystem management (HUANG et al., 1992). Nevertheless, we could not find the expected spatial justification for the *h-d* tendencies (PENG et al., 2004), once locations which are closely related, such as Canoinhas and Três Barras, near one another, had different *h-d* tendencies. This is due to extremely local environmental characteristics and a heavier sampling grid would guarantee these points to be smoothed in relation to other nearby locations.

Even though we had few data points in the correlation analysis among environmental variables and fitted *h-d* coefficients, the following results are also based on field observations and literature patterns. There were positive correlations between the asymptote and mean annual total precipitation in even-aged plantation forest (weak correlation) and especially uneven-aged natural forest (strong correlation). This fact corroborates the affirmation that water availability plays a major role in potential height development (YORK et al., 2003; KOCH et al., 2004; WANG et al., 2006). Furthermore, we found negative correlation between the asymptote and location altitudes, for even-aged plantation forest (strong correlation) and uneven-aged natural forest (moderate correlation). This is a known relationship in temperate forest areas, where trees grow less in higher altitudes (PAULSEN et al., 2000; COOMES; ALLEN, 2007), and have lower heights (PAULSEN et al., 2000).

CONCLUSIONS

The Michailoff's model showed good fit for the height-diameter relationship of *A. angustifolia*, with R^2 between 0.55 and 0.80;

The same *h-d* model may be used for trees growing in plantations and in natural forests, but open-grown trees need an own *h-d* model;

Some locations may be grouped by *A. angustifolia* *h-d* relationship, but no specific spatial pattern could be determined;

However, there was correlation between *h-d* models parameters and ecological variables, which does indicate the existence of a spatial pattern.

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