PREDICTING ANNUAL STEM DIAMETER INCREMENT OF MAJOR TREE SPECIES IN MIXED HILL DIPTEROCARP FOREST WITH CONSIDERATION ON TREE AND STAND LEVEL EFFECTS

K Abd Rahman[1,] *, M Muhammad Afizzul[1], K Niiyama[2], S Iida[3], K Kimura[4], T Sato[5], ZS Nurhajar[1], M Samsudin[1], H Ismail[1] & R Azizi[6]

[1]*Forest Research Institute Malaysia, 52109 Kepong, Selangor, Malaysia*
[2]*Bureau of International Partnership, Forestry and Forest Products Research Institute, Tsukuba, Ibaraki 305-8687, Japan*
[3]*Department of Plant Ecology, Forestry and Forest Products Research Institute, Tsukuba, Ibaraki 305-8687, Japan*
[4]*Faculty of Symbiotic Systems Science, Fukushima University, Kanayagwa 1, Fukushima City, Fukushima 960-1296, Japan.*
[5]*Department of Forest Vegetation, Forestry and Forest Products Research Institute, Tsukuba, Ibaraki 305-8687, Japan*
[6]*Green Forest Resources, Rawang 48000, Selangor, Malaysia*

**rahmank@frim.gov.my*

ABD RAHMAN K, MUHAMMAD AFIZZUL M, NIIYAMA K, IIDA S, KIMURA K, SATO T, NURHAJAR ZS, SAMSUDIN M, ISMAIL H & AZIZI R. 2016. Predicting annual stem diameter increment of major tree species in mixed hill dipterocarp forest with consideration on tree and stand level effects. Predicting tree species growth for tropical forests is a challenging task for forest researchers due to an insufficient number of samples needed to run the classical fixed-effects regression method. The aim of the paper was to develop a predictive model for annual diameter increment of a multispecies hill dipterocarp forest stand. To address this issue, a linear mixed-effects model was applied to predict the diameter at breast height (dbh) annual increment of trees that treated species as a random effect. A random coefficient for the predictor variables, which included tree size and competition parameters was examined. Basic models using dbh and natural logarithm of dbh or log(dbh) were tested by treating the species random effects at various combinations of the predictor variables. The basic model that was selected contained random coefficients for intercept terms, dbh and log(dbh). Subsequent predictor variables depicting the effects of competition from surrounding trees, trees smaller or larger than the subject trees, and a structure component represented by maximum dbh, were tested. The final model contained the predictors dbh, log(dbh), stocking density, maximum dbh and competition from trees smaller than the subject tree.

Keywords: Annual dbh increment, random effects, multispecies

INTRODUCTION

Tropical mixed forests are characterised by a large number of species with diverse growth habits. The huge challenge in this forest type has been constructing models for species groups with similar growth patterns. It is often regarded as impractical to develop reliable growth equations for each species due to the small number of observations for most species and lack of identification to species level.

Wan Razali (1986) developed growth equations for five commercial species groupings recognised by the Forestry Department of Peninsular Malaysia. These five groups were the dipterocarp group, and four non-dipterocarp groups: light hardwoods, medium hardwoods, heavy hardwoods and other miscellaneous species. The miscellanous species group comprised lesser-known species and species with no significant commercial timber value. Using commercial species grouping in modelling predictions of diameter at breast height (dbh) increment has also been investigated for an eight commercial species grouping (Ismail et al. 2005). Chai and LeMay (1993) developed a diameter-increment model that was fitted for three modelling levels, i.e. individual species, two groups of species (light-demanding vs shade-tolerant) and one group of all species combined. Modelling at the individual–species level gave only a slight gain in predictive power compared with the one-group level. No gain was obtained for the two-group level compared with the one-group level. Ong and Kleine (1995) developed a diameter-increment model for individual tree species or species groups (identified by generic name) that were sufficiently represented in the database. However, a given genus may represent a single species or a large number of species. Rare species were assigned to a group based on general knowledge of their silvicultural behaviour and growth rates. Vanclay (1991) presented a two-stage approach using pairwise F-tests to compare and aggregate a large number of species into a more manageable number of groups. The resulting regression models exhibited homogenous variance for those species with the most data but homogeneity decreased for species with fewer data. Species were ranked by the number of remeasurements available for each species. This method provided better predictive power than other models based on subjectively-formed groups.

Recent findings by Iida et al. (2012) indicated that the demographic performance of trees in a multispecies stand in a primary dipterocarp forest was linked with architectural traits such as adult stature, wood density and capacity for horizontal crown expansion. This may also help to explain the differences in growth patterns seen among trees in the forest.

The hypothesis explored here is that the diameter growth of individual trees in primary hill dipterocarp forests can be gainfully modelled by treating species as a random effect in a mixed-effect regression model. Abd Rahman (2002) explored the application of linear and non-linear mixed-effects models with species as random effects for predicting annual diameter at breast height (dbh) increment for managed second growth hill dipterocarp forest. A mixed-effects model has several advantages: (1) the model form is common to all species, with slight perturbations to each parameter arising from the random species effect, (2) all data are used in a single estimation algorithm and (3) in a simulation context varying levels of resolution with respect to species or species grouping can be accommodated by the same equation (Abd Rahman 2002)

Recently, Abd Rahman and Nur Hajar (2013) applied the mixed-effects modelling to predict commercial tree volume for multispecies stand of second growth forest. However, both Abd Rahman (2002) and Abd Rahman and Nur Hajar (2013) used local names instead of species. The local name of trees may represent more that one species of the same genus or even family and their behaviour may not be the same among the species. Wan Razali et al. (2015) applied the mixed-effects approach to model early height growth of planted tree species in Sarawak. However, this is limited to five selected species and for species with more than 50 plants only.

The aim of this paper is to develop a predictive model for annual diameter increment of a multispecies stand of mixed hill dipterocarp forest. A linear mixed effects regression model was adopted that treated species as the group factor or random effect. Random coefficients for the predictor variables, which included tree size and competition parameters, were examined.

MATERIALS AND METHODS

Site description

The data used for this study were gathered from a 6-ha (200 m × 300 m) ecological plot (3° 37' N, 101° 44' E; Figure 1) located in Compartment 30 of Semangkok Forest Reserve, Peninsular Malaysia. Semangkok Forest Reserve, located about 60 km north of Kuala Lumpur, is a virgin jungle reserve surrounded by second-growth forest that was selectively logged in the 1980's (Niiyama et al. 1999). The 6-ha ecological plot (Figure 1), which was established in 1992, contains a narrow ridge and steep slope covered with a typical hill dipterocarp forest. This forest type is characterised by the predominance of large trees of *Shorea curtisii*, which is semi-gregarious, and undergrowth of a stemless palm, *Eugeissona tristis*, which frequently form dense thickets. Surface soil chemical properties are influenced by topography and soil moisture regimes–the thin surface soil on the ridges and convex slopes has a low pH, high carbon, nitrogen and available phosphoric acid content, and high C/N ratios (Tange et al. 1998). The average annual rainfall is 2414 mm and the average annual minimum and maximum temperatures ranges between 21.9–33 °C (Saifuddin et al. 1991).

In 1992, all trees with dbh > 5 cm in the 6-ha plot were tagged and information collected on tree status (living or dead), species and dbh. Censuses were taken at irregular intervals (1992, 1993, 1995, 1997, 1999, 2001, 2003 and 2007) giving a total of eight censuses in the 17 year period from 1992 till 2007. The data set was derived from the eight censuses combined. Only trees that survived at both censuses were used for predicting the annual dbh increment analysis. We conducted the analysis for all trees with dbh > 5 cm. We identified outliers as trees showing unlikely large negative (> 2.5% of prior year's dbh) and large positive (> 5 cm) annual dbh growth, and excluded these trees from the dataset. Remaining trees showing negative

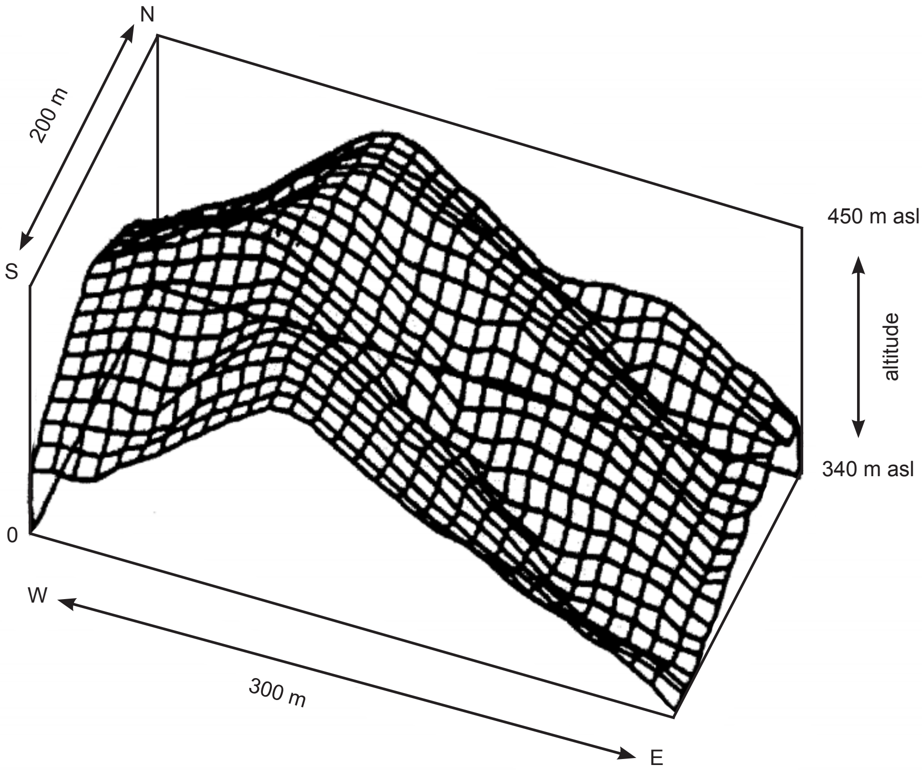

Figure 1 Topography of the 6-ha ecological hill dipterocarp forest plot in Semangkok Forest Reserve; asl = above sea level

growth (< 2.5% of prior year's dbh) were assumed to have zero growth for that year. A total of 6% of 38,954 records was excluded, leaving a total of 36,616 trees in the final data set (Table 1). From this data set, 10 most abundant species in the plot were selected to illustrate the growth pattern among species (Table 2).

Data structure

The independent variables were grouped into stand- and tree-level attributes. The stand-level attributes were measures of size structure: maximum dbh (cm) and stocking density: (1) stand basal area (SBA, m^2 ha^{-1}) where SBA = $\sum (p_i \, dbh_i^{\,2}) / 40000$, and (2) stand density index (SDI) where SDI = $\sum (dbh_i / 25.4)^k$, k = 1.6, 2.0 or 2.6, assuming maximum size-density slopes of 1.6, 2.0 and 2.6. The tree-level attributes were measures of tree size: dbh and natural logarithm of dbh, and competition indices: (1) competing stand basal area (SBA_C) and (2) competing stand density index (SDI_C) assuming maximum size-density slopes of 1.6, 2.0 and 2.6.

The SBA_C and SDI_C of the subject tree assumed that trees smaller than the subject tree are competing with the subject tree for growing space. The calculation of SDI_C was based on the maximum size-density concept and the contribution of individual trees to total SDI (Reineke 1933, Long & Daniel 1990). The exponent represents the slope of the maximum size-density line. A higher maximum size-density slope confers a greater value if dbh > 25.4 cm but a lower value if dbh < 25.4 cm. When dbh = 25.4 cm, all values are equivalent. The slope of 1.6 is consistent with Reineke's (1933) original results for many species, and the slope of 2.0 implies that SDI and stand basal area are equivalent. The highest slope of 2.6 was derived empirically for mixed dipterocarp forests of Peninsular Malaysia (Abd Rahman 2002).

Model selection and statistical analysis

Instead of adopting the fixed-effects model, we used a mixed-effects model with species random effects. It has the advantages of the model form that is common to all species, with slight perturbations to each parameter arising from the random species effect (Abd Rahman 2002). In mixed-effects models, the random

Table 1 Summary statistics for the data used to develop the periodic annual increment in a diameter at breast height (dbh) model for hill dipterocarp forest stands in Peninsular Malaysia

Variable	Variable code	Mean	SD	Min	Max
Periodic annual dbh increment (cm year^{-1})	dinc	0.2	0.3	0.0	5.0
dbh (cm)	dbh	16.9	17.2	5.0	227.0
Stand basal area (m^2)	SBA	0.1	1.0	0.0	4.1
Stand density index (SDI) at slope 1.6	$SDI_{1.6}$	26.9	46.0	2.6	68.4
SDI at slope 2.0	$SDI_{2.0}$	33.0	11.5	1.6	131.2
SDI at slope 2.6	$SDI_{2.6}$	54.0	18.8	0.8	406.8
Competing basal area (m^2)	SBA_C	0.2	0.3	0.0	3.2
Competing SDI at slope of 1.6	$SDI_{C1.6}$	4.5	5.5	0.0	48.7
Competing SDI at slope of 2.0	$SDI_{C2.0}$	3.7	5.7	0.0	62.5
Competing SDI at slope of 2.6	$SDI_{C2.6}$	3.2	7.4	0.0	115.2
Maximum dbh (cm)	dmax	11.2	33.0	25.1	227.0

SD = standard deviation, Min = minimum, Max = maximum

Table 2 Summary statistics for diameter at breast height (cm) of tree species used in the fitting dataset

Species	Species code	No. of trees	Mean	SD	Min	Max
Shorea curtisii	SHORCU	1915	36.9	37.6	5.0	162.0
Lithocarpus wallichianus	LITHWA	1115	19.8	10.5	5.0	53.7
Teijsmanniodendron coriace	TEIJCO	886	15.1	8.9	5.0	43.8
Scaphium macropodum	SCAPMA	676	29.3	24.0	5.0	106.0
Anisoptera curtisii	ANISCU	629	29.7	27.2	5.1	129.0
Pimelodendron griffithianum	PIMEGR	465	16.1	9.6	5.0	42.0
Diospyros sumatrana	DIOSSU	206	10.6	4.1	5.0	23.6
Shorea leprosula	SHORL1	178	47.8	36.8	5.1	147.0
Parkia speciosa	PARKSP	100	32.1	22.3	5.3	79.2
Endospermum diadenum	ENDOMA	67	19.1	15.0	5.1	52.3

SD = standard deviation, Min = minimum, Max = maximum

effect is assumed to be a random draw from some population of possible coefficients (Littell et al. 1996). In this case, the regression model for each species is assumed to be a random deviation from some population of regression models. Species was also expected to influence the slope of at least some of the predictor variables (Abd Rahman 2002) so an expanded model was formulated as follows:

$$Y_i = X_i\alpha + Z_i\delta + e_i$$

where $Y_i = n_i \times 1$ vector of observations for species group i, $X_i = n \times p$ matrix of predictor variables for species group i, $Z_i = n \times p$ matrix of predictor variables, $\delta = n_i \times 1$ vector of the random species effect, $e_i = n_i \times 1$ vector of random errors, i = 1,2,3,….,q, q = number of species groups, n_i = number of observations in species group i, α = p-dimensional vector of fixed effects.

Application of basic model

The basic model contained two measures of tree size, i.e. dbh and log(dbh) as predictor variables. The response variable was the periodic annual diameter increment for each individual tree, which was calculated as the difference between dbh size at the start and end of the growth period, divided by the time period between measurements. The model has the desirable property of allowing for a peaking behaviour and a long-term asymptotic approaching zero, and the long right hand tail on the increment curve function accomodates the very slight but continued increment accrued by large trees (Vanclay 1994).

Four basic models were tested by applying the random coefficient at the intercept terms and/or dbh and/or natural logarithm of dbh (Table 3). The four models were compared using the likelihood ratio statistical test (Pinheiro & Bates, 2000).

Selection of predictor variables

We extended the basic linear mixed-effects model to include the predictor variables with regard to total stocking density and the competing stocking density (Table 4). For this analysis, we selected the following predictor variables taking into account the logical behaviour of growth over predictors. Five predictors were selected in the chosen model. The predictors implied the effects of tree size (dbh and natural logarithm of dbh), competition, stand density and indicators of size structure. The combined effect of initial tree dbh and its natural logarithm has the desirable property of of allowing a peaking behaviour and asymptotic approach to zero as tree size increases toward a maximum. Increasing competition from above or below and increasing stand density have a negative influence on diameter increment. Negative parameter estimates for stand density and competing stand density imply that an increase in dbh increment can be expected with a reduction in stand density or competition. Our preliminary analysis indicated that the competition based on competing stocking density from below gave the expected negative sign parameters or effects on dbh growth.

Size structure of the forest stand is represented in part by maximum dbh which implies that growth of a given tree is greater when maximum dbh is larger. The implied greater variability in vertical structure may indicate that light from low sun angles early and late in the day is more available under this condition (Abd Rahman 2002).

Table 3 Four types of of basic linear mixed-effects models tested

Model	Linear mixed-effects model
1	$\ln(\text{dinc} + 0.02)_{ij} = (\alpha_0 + \delta_{0i}) + \alpha_1 \text{dbh} + \alpha_2 \log(\text{dbh}) + e$
2	$\ln(\text{dinc} + 0.02)_{ij} = \alpha_0 + \delta_{0i} + \alpha_1 \text{dbh} + (\alpha_2 + \delta_{2j}) \log(\text{dbh}_{ij}) + e$
3	$\ln(\text{dinc} + 0.02)_{ij} = \alpha_0 + \delta_{0i} + (\alpha_1 + \delta_{1i}) \text{dbh}_{ij} + \alpha_2 \log(\text{dbh}) + e$
4	$\ln(\text{dinc} + 0.02)_{ij} = \alpha_0 + \delta_{0i} + (\alpha_1 + \delta_{1i}) \text{dbh}_{ij} + (\alpha_2 + \delta_{2j}) \log(\text{dbh}_{ij}) + e$

dinc = periodic annual dbh increment, α = fixed coefficient parameter estimate, δ = random coefficient parameter estimate, dbh = diameter at breast height

Table 4 Expanded linear mixed-effects models for predicting periodic annual diameter increment that incorporated tree size and stocking density variables, maximum diameter at breast height (dbh) and competing stand density

Model	Linear mixed-effects model
5	$\ln(\text{dinc} + 0.02)_{ij} = \alpha_0 + \delta_{0i} + (\alpha_1 + \delta_{1i}) \text{dbh}_{ij} + (\alpha_2 + \delta_{2j}) \log(\text{dbh}_{ij}) + \alpha_3 \text{SBA} + \alpha_4 \text{dmax} + \alpha_5 \text{SBA}_C + e$
6	$\ln(\text{dinc} + 0.02)_{ij} = \alpha_0 + \delta_{0i} + (\alpha_1 + \delta_{1i}) \text{dbh}_{ij} + (\alpha_2 + \delta_{2j}) \log(\text{dbh}_{ij}) + \alpha_3 \text{SDI}_{1.6} + \alpha_4 \text{dmax} + \alpha_5 \text{SDI}_{C1.6} + e$
7	$\ln(\text{dinc} + 0.02)_{ij} = \alpha_0 + \delta_{0i} + (\alpha_1 + \delta_{1i}) \text{dbh}_{ij} + (\alpha_2 + \delta_{2j}) \log(\text{dbh}_{ij}) + \alpha_3 \text{SDI}_{2.0} + \alpha_4 \text{dmax} + \alpha_5 \text{SDI}_{C2.0} + e$
8	$\ln(\text{dinc} + 0.02)_{ij} = \alpha_0 + \delta_{0i} + (\alpha_1 + \delta_{1i}) \text{dbh}_{ij} + (\alpha_2 + \delta_{2j}) \log(\text{dbh}_{ij}) + \alpha_3 \text{SDI}_{2.6} + \alpha_4 \text{dmax} + \alpha_5 \text{SDI}_{C2.6} + e$

dinc = periodic annual dbh increment (cm year^{-1}), SBA = stand basal area, SDI (for values 1.6, 2.0, 2.6) = stand density index (for the stated maximum size-density slope values), SBA_C = competing SBA, SDI_C (for values 1.6, 2.0, 2.6) = competing SDI (for the stated maximum size-density slope values), α = fixed coefficient parameter estimate, δ = random coefficient parameter estimate

Assessment of growth behavior

The biological behaviour of dbh growth as implied by the final model was examined for 10 selected species. Our main aim was to demonstrate the sensitivity dbh increment pattern of different species over different predictor variables.

All data management and preparation was conducted using R software version 3.2.3 (2015) while data analysis was carried out by linear mixed-effects models (nlme package in R software version 3.1-122 (Pinheiro et al. 2015)). We used Rstudio version 0.99 (2015) to write the R script and run the analysis.

RESULTS AND DISCUSSION

Statistical significance of the basic model

Model 4 gave the lowest AIC value (Table 5). The likelihood ratio test also indicated that Model 4 was significantly different than Models 1, 2 and 3 (Table 6). Based on the results, we chose Model 4 as the basic model by which to identify other possible variables needed to predict annual dbh increment.

Relative performance of alternative parameters on the size-density limit

The stand density index is derived by summation of individual trees within the plot. Model 6, which contained the predictor variables SDI and BA for the maximum size-density slope of 1.6, received the lowest AIC score, indicating that this model gave the best fit for the data (Table 7). The maximum size-density slope of 1.6 is consistent with Reineke's (1933) results for many species, while the slope of 2.0 implies a fixed basal area. The results imply that the diameter increment of trees in second growth forest can be best explained by a lower maximum size-density slope value than is applied for primary mixed dipterocarp forest.

The scatter plot dbh and natural logarithm of dbh and other selected predictor variables ($SDI_{1.6}$, dmax, $SDI_{C1.6}$) did not show obvious bias to the residuals (Figure 2). Based on this finding, we decided to adopt the linear mixed-effects approach to develop the individual tree dbh growth equation.

Table 5 Parameter estimates and standard errors for four basic linear mixed-effects models for periodic annual diameter increment based only on tree diameter at breast height (dbh) and ln(dbh)

Parameter estimate	Model 1		Model 2		Model 3		Model 4	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
α_0	-3.325	0.048	-3.360	0.080	-3.380	0.116	-3.318	0.117
α_1	-0.004	0.001	-0.012	0.001	-0.011	0.004	-0.012	0.564
α_2	0.493	0.020	0.545	0.036	0.551	0.067	-0.048	0.006
AIC	73731		73198		73091		73041	

SE = standard error, all parameters are significant at p = 0.05; the basic model refers to the predictors comprising only dbh as the variable

Table 6 Comparison of four basic models by Akaike Information Criterion (AIC) and the Likelihood Ratio (LR) Test for periodic annual diameter increment

Model	df	AIC	LR Test	
			Test	LR
1	5	108676		
2	7	107898	1 vs 2	782.45**
3	7	107758	2 vs 3	
4	10	107604	3 vs 4	160.07**

df = degree of freedom, ** = significant at $p < 0.001$

Table 7 Parameter estimates and standard errors for the four expanded linear mixed-effects models for periodic annual diameter increment

Parameter estimates	Model 5		Model 6		Model 7		Model 8	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
α_0	-3.459	0.106	-3.390	0.107	-3.459	0.106	-3.432	0.107
α_1	-0.008	0.004	-0.009	0.004	-0.008	0.004	-0.008	0.004
α_2	0.518	0.062	0.541	0.062	0.518	0.062	0.500	0.063
α_3	-0.130	0.012	-0.012	0.001	-0.007	0.001	-0.001	0.000
α_4	0.002	0.000	0.003	0.000	0.002	0.000	0.001	0.000
α_5	-0.184	0.051	-0.009	0.003	-0.009	0.003	-0.006	0.002 $^{n.s.}$
AIC	108080		107982		108092		108219	

SE = standard error, n.s. = not significant at $p < 0.001$, all other parameter estimates showed significant p-values; model equations given in Table 3

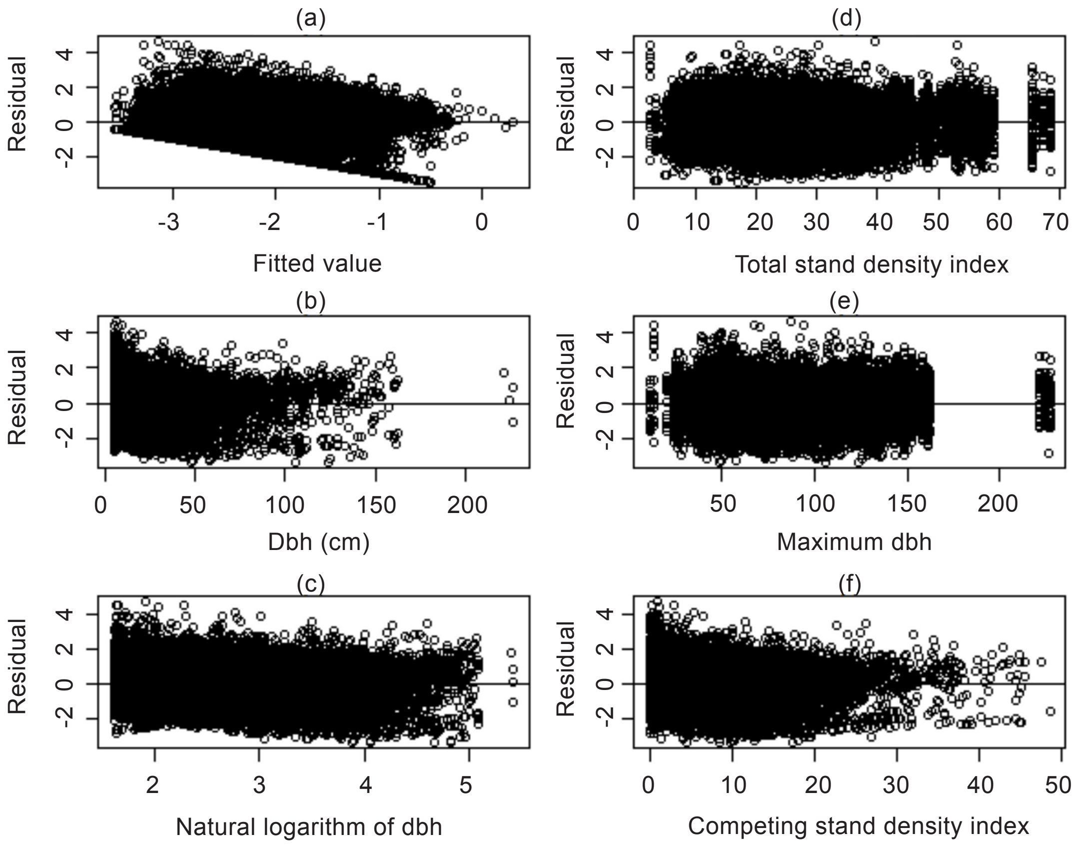

Figure 2 Scatterplots of residuals vs (a) predicted dbh increment, (b) dbh, (c) natural logarithm of dbh, (d) total stand density index (SDI), (e) maximum dbh and (f) competing stand density index ($SDI_{C1.6}$) using Model 6

Assessment of growth behaviour

Biological behaviour of the periodic annual dbh increment model

The predicted average annual dbh increment over the various dbh sizes differed between species (Figure 3). Fast-growing species that grow to large, mature trees may behave differently than slow-growing species. The differences also reflected the maximum tree size the trees may grow to mature stage. For almost all species, growth rates increased rapidly at the initial stage then slowed to eventually reach a maximum growth rate, which differed among the species, and thereafter declined. Among the 10 species, *Shorea leprosula* showed a higher growth rate across dbh class, reaching its maximum growth rate at 79 cm dbh. *Shorea curtisii* grew at a slower rate and reached the maximum growth rates at 53 cm dbh. Another dipterocarp, *Anisoptera curtisii* reached the maximum at 60 dbh with much slower growth rates (Figure 3).

Further, we examined the potential maximum growth of the 10 species under no-competition conditions by treating SDI, SDI and maximum tree dbh equal to the dbh of the subject tree. We noticed that under no-competition conditions, *S. leprosula* maximum dbh growth rate of 0.78 cm per year was predicted at 105 cm dbh while for *Shorea curtisii* the maximum growth rate of 0.55 cm per year was predicted at 73 cm dbh (Table 8). The results indicated that under dominant conditions, trees will continue to grow faster than average (Figure 3) and the maximum growth occurs at larger dbh sizes. The different dbh values at which respective tree species achieve their maximum growth rates can be used as the basis for species-specific felling size recomendations (Table 8). From a silvicultural viewpoint, foresters may need to intervene to enhance dbh growth by removing surrounding trees to reduce competition to subject trees.

Effects of stand density index on growth

The growth of trees was expected to vary based on the available growing space or at different competition levels from the surrounding trees. We simulated the growth of the 10 selected species trees as free of competition when $SDI_{C1.6}$ is equal to zero. In the model, the condition was exemplified when the tree dbh was that of the largest tree within the stand, i.e. the tree with the maximum dbh. The predicted dbh annual increment decreased with increasing SDI among the species.

The growth response of trees with 20 cm dbh across SDI differed among species. Using similar conditions set for competition-free tree growth as above, we noticed that the growth trend showed marked differences when the competition was the lowest and decreased with increasing SDI (Figure 4).

CONCLUSIONS

A random-effects model for individual tree periodic annual dbh increment was explored using data from 10 selected tree species in a primary hill dipterocarp forest plot. The covariates selected for the analysis reflected tree size, competition and stand size variability. Random species effects allowed estimation of the

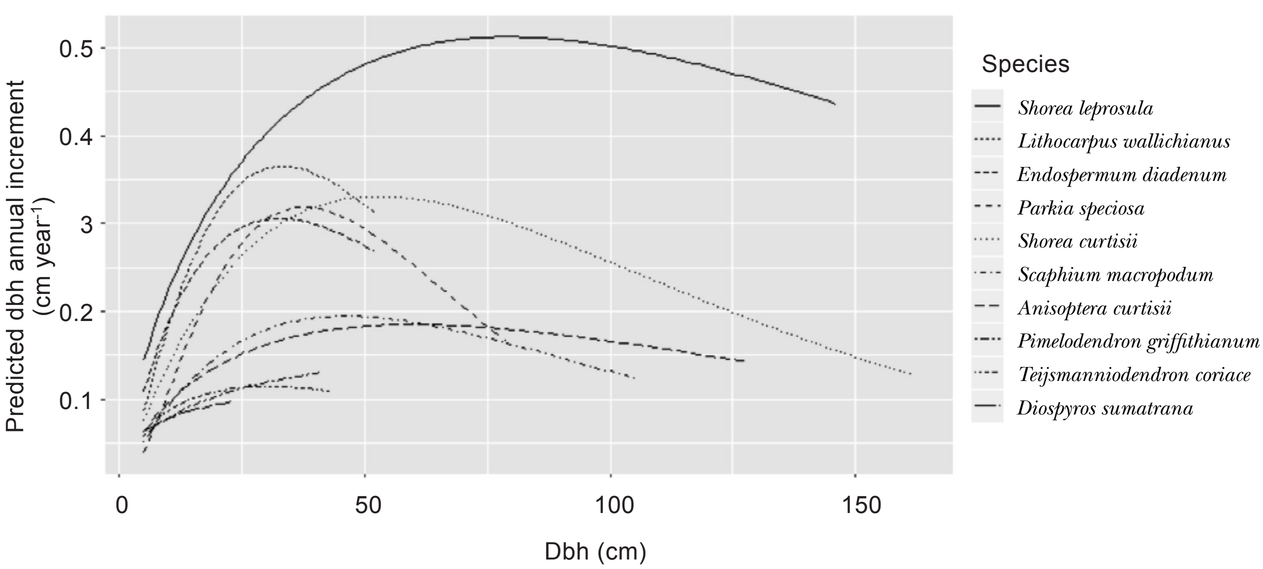

Figure 3 Average predicted periodic annual diameter at breast height (dbh) increment by Model 6 for selected forest tree species in relation to dbh

Table 8 The diameter at breast height (dbh) of 10 selected tropical forest tree species at their respective maximum annual dbh increment rates, and the largest tree (dbh) in the 6-ha plot for that species

Species	Dbh (cm) at maximum growth	Maximum growth (cm year^{-1})	Maximum dbh (cm)
Shorea leprosula	105	0.78	146.7
Lithocarpus wallichianus	40	0.52	53.7
Endospermum diadenum	36	0.43	52.3
Parkia speciosa	42	0.45	79.2
Shorea curtisii	73	0.55	162.3
Scaphium macropodum	61	0.29	106.3
Anisoptera curtisii	107	0.34	128.7
Pimelodendron griffithianum	42	0.17	42.0
Teijsmanniodendron coriace	42	0.16	43.8
Diospyros sumatrana	24	0.26	23.6

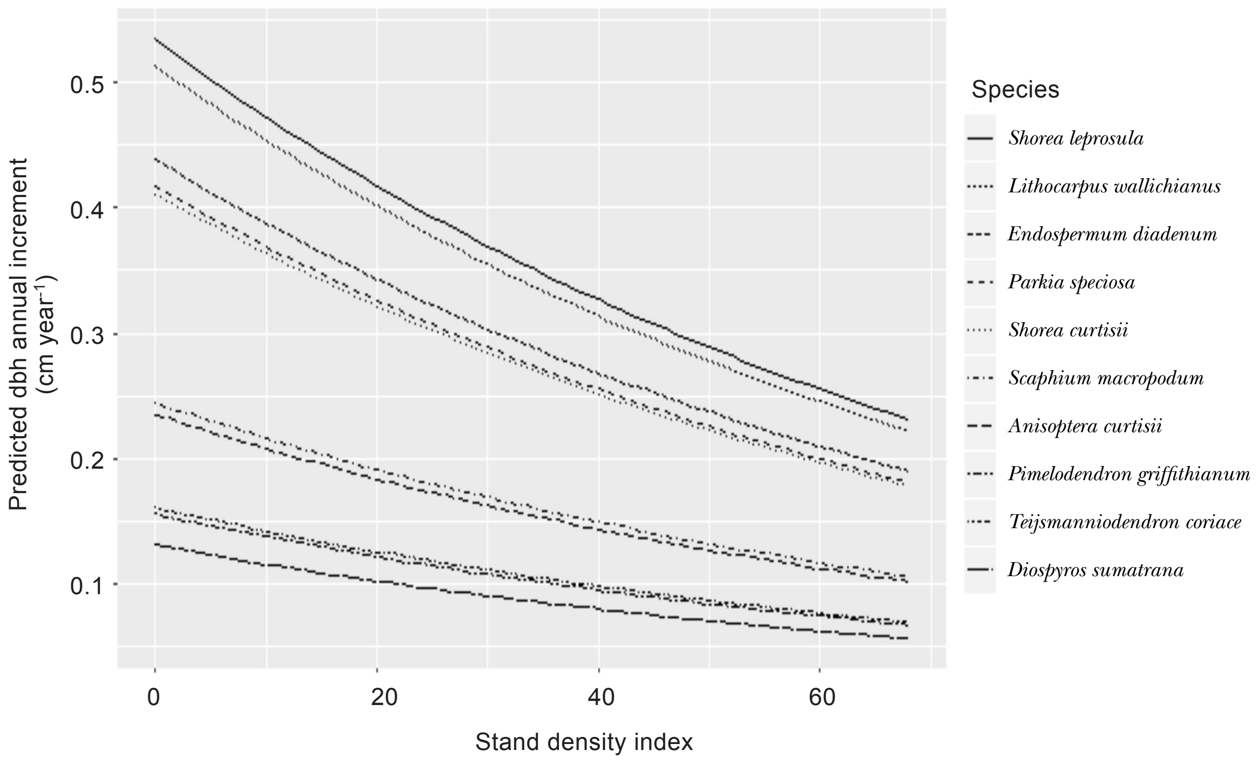

Figure 4 Predicted periodic annual dbh increment in relation to $SDI_{C1.6}$ for open-grown 20 cm dbh trees of 10 selected species using Model 6

mean and variance of each species relative to the population of all species. Species effects on tree size covariates allowed the curve to deviate from the population mean and to reflect the unique behaviour of individual species. The mixed model approach also enabled reliable estimation of species-specific parameters simultaneously and thus made it possible to develop a growth equation for all species simultaneously in a single estimation algorithm.

Random coefficients may be used for species aggregation and can be explored further. The model can be incorporated into a stand dynamic empirical model to project future growth of a primary hill dipterocarp forest. The model may be further improved by applying the non-linear mixed-effects approach. The correlation among trees within a plot and among repeated observations within a single tree over time was however not addressed in the analysis.

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