


AN ABSTRACT OF THE THESIS OF

Abd. Rahman Kassim for the degree of Doctor of Philosophy in Forest Resources presented on March 9, 2001. Title: Growing Stock Assessment and Growth Prediction System for Managed Hill Dipterocarp Forest of Peninsular Malaysia.

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Abstract approved

 Douglas A. Maguire

The silviculture of mixed dipterocarp forests of Peninsular Malaysia can potentially be improved by developing quantitative tools and guidelines for this forest type. This thesis addresses three key objectives; 1) to test the hypothesis that a maximum size-density relationship can be identified in hill dipterocarp forests of Peninsular Malaysia, 2) to develop growth equations for predicting annual diameter or basal area increment from initial stand structure and tree conditions, and 3) to develop guidelines for applying the maximum size-density concept to growing stock assessment and control in hill dipterocarp forest. Data from temporary and permanent sample plots were examined to test the applicability of the maximum size-density concept. The maximum size-density limit in mixed dipterocarp forests was related to stand structure as described by the skewness and variance of dbh^m . Relatively little of the variation in maximum size-density limits was attributable to species composition as represented by different community types. Temporary plots did not allow for the assessment of the maximum size-density limit, at least at the spatial scale investigated. In contrast, data from long-term permanent sample plots indicated that the maximum size-density limit was quite consistent. Several stand trajectories deviated from the limit for short periods, but returned to the same limit after a few years. Silvicultural guidelines were developed by applying the maximum size-density concept a stand density index approach took into account the residual stocking, allocation of growing stock by size class, and species mixture before and after treatment. Appropriate silvicultural strategies involving stand density manipulation require considerable insight into future stand development, especially the competitive effects at both the tree and stand level, and this effort requires

quantitative assessment of tree growth through statistical modeling. A mixed-effects model with a random species effect was applied for modeling individual tree dbh increment. This model was compared with classical fixed effects models using data from second growth hill dipterocarp forest. The mixed-effects model offered the advantage that all species could be run simultaneously in one equation, and also allowed variation in slope for each species when an interaction between random species effects and other covariates were included in the model. Diameter growth was a function of tree size, inter-tree competition, and stand structure.

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Growing Stock Assessment and Growth Prediction System for Managed Hill Dipterocarp
Forest of Peninsular Malaysia

by

Abd. Rahman Kassim

A THESIS

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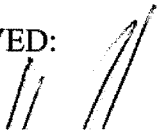
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"By time. All mankind are in great loss, except those who believe, and do righteous deed, and reminding on truth and reminding in patience"

Verse:Al-Asr

CONTRIBUTION OF AUTHORS

Dr. Douglas A. Maguire was involved in the design, analysis and editing of each manuscript. Mr. Shahrulzaman Idris assisted in the field data collection and data management of the study.

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GROWING STOCK ASSESSMENT AND GROWTH PREDICTION SYSTEM FOR MANAGED HILL DIPTEROCARP FOREST OF PENINSULAR MALAYSIA

CHAPTER 1

INTRODUCTION

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INTRODUCTION

A variety of silvicultural systems has been applied to dipterocarp forest, depending on markets, technological changes, land-use patterns, labor cost etc. In general these silvicultural systems can be broadly classified into the classical Shelterwood System (monocyclic) and Selection System (polycyclic) (Appanah, 1997). In Peninsular Malaysia, both silvicultural systems have been practiced with some modifications to manage dipterocarp forests. Details of these silvicultural systems have been described by Wyatt-Smith (1962) and Thang (1987). These systems have evolved over time, with name changes to reflect their differing strategies (Table 1). Currently, the dipterocarp forest which forms the bulk of the production forest within the Permanent Forest Estate is managed under two systems, namely the Modified Malayan Uniform System (MMUS) on a 55 year cutting cycle, and the Selective Management System (SMS) on a 30 year cutting cycle (Thang 2000). These silvicultural systems were primarily designed for managing primary dipterocarp forests, but most of the production forest is confined to hillier regions. Introduction of mechanized harvesting to hill dipterocarp forest has altered the stand structures, species composition, spatial distribution, and stocking, resulting in a more heterogeneous residual stand. These changes demand a more flexible silvicultural system for managing second growth dipterocarp forest to ensure the sustainability of timber yield, as well as other ecological functions and services. The experience from a variety of silvicultural practices in Peninsular Malaysia (Table 1) provides opportunities for the research silviculturist to explore impacts of different silvicultural manipulations, including timber harvesting, on targets of management, thereby improving our decision-making ability.

NEED FOR QUANTITATIVE SILVICULTURAL GUIDELINES IN MIXED DIPTEROCARP FOREST

In principle, the productivity of managed forests can be improved through silvicultural practices, such as control of stand structure, alteration of developmental processes, control of species composition, control of stand density, restocking of unproductive areas, control of rotation length, facilitation of harvests and conservation of site productivity (Smith et al.1997). The first three silvicultural activities are very important determinants of stand productivity and can be manipulated directly by foresters, provided a quantitative assessment of the growing stock is available. Although quantitative guidelines have been developed for many temperate forests, the principles may apply to mixed dipterocarp forest of Peninsular Malaysia as well.

Control of stand density for a given silvicultural objective requires knowledge of the maximum carrying capacity of the target stand (Smith et al. 1997). In some temperate forests, knowledge of maximum density is quite well established and its potential for assessing appropriate growing stock levels has been explored and applied to both even-aged (Reineke, 1933; Long, 1985; Long, 1996) and uneven-aged stands (Long and Daniel, 1990; Cochran, 1992), as well as to mixed species stands (Sterba and Monserud, 1993). In uneven-aged stands, allocation of growing stock to different size classes has been based on the maximum carrying capacity of the site (Long and Daniel 1990; Cochran, 1992). The manipulation of growing stock, and ultimately stand structure, is frequently specified as part of the forest management objectives (see Lilieholm et al. 1994; Fieldler and Cully, 1995; Anhold et al. 1996).

Maximum size-density relationships are still new in the tropics. Although density management has been applied in teak plantations (Kumar and Long, 1995), and Hummel (2000) advocated the application of maximum size-density relationships to tropical forests, application of the maximum size-density concept to

management of mixed tropical forest has not been explored. In one extension beyond single-aged pure stands, Sterba and Monserud (1993) demonstrated that maximum size-density limits or available growing space is influenced by stand structural parameters and habitat type in uneven-aged, mixed-species temperate forests. These findings lead one to expect similar relevance to structurally-diverse, mixed-species stands of dipterocarp forest.

Control of rotation length requires information on the optimum yield and stand structure that should be left growing after harvest (Smith et al. 1998). In the tropics for example, Baur (1965 cited in Dawkins and Philips, 1998) suggested that for rapid diameter growth response in tropical rainforest, stocking density by basal area should be reduced from $30 \text{ m}^2 \text{ ha}^{-1}$ to $10 \text{ m}^2 \text{ ha}^{-1}$, a reduction of 67 % from the maximum stand basal area. In dipterocarp forest Tang and Wan Razali (1981) reported a positive correlation between logging intensity as percent of the original basal area removed during logging, and mortality rate and severity of logging damage during the first five year period after logging. Assessment and control of level of growing stock together with development of a prediction system would provide quantitative guidelines for estimating optimum yield, desired stand structures and species composition. Information on the maximum carrying capacity for a particular stand is also required to more reliably and realistically estimates sustainable yield. For example, Hann and Wang (1990) combined equations for individual tree mortality rates with maximum density limits to constrain projected size-density trajectories so that they approach but do not exceed their maximum density line.

NEED FOR GROWTH PROJECTION MODELS IN MIXED DIPTEROCARP FOREST

Individual tree-based growth prediction system for the dipterocarp forest of Peninsular Malaysia is generally lacking, although some effort has been carried out in the past. Wan Razali (1986, 1988) presented individual-tree diameter growth and mortality models for dipterocarp forests harvested under the Malayan Uniform System. Yong (1990) reported growth and yield functions for different species groups and diameter classes using three stand variables, including number of trees, basal area of trees and gross volume. He used these functions to predict the future yield of all trees greater than 30 cm dbh. Recently, effort has been made by the Forest Department of Peninsular Malaysia to modify the individual tree-based growth model called DIPSIM, which was developed for Sabah dipterocarp forest (Ong and Kleine, 1995). This model is being calibrated for yield regulation of the mixed dipterocarp forest in Peninsular Malaysia.

An extensive amount of data is available for developing empirical growth models for dipterocarp forest of Peninsular Malaysia. Many permanent sample plots have been established to monitor silvicultural experiments, and continuous forest inventory (CFI) plots have been maintained in virgin and second growth forests throughout Peninsular Malaysia since the 1970's, with the aim to produce reliable estimates of tree growth and stand dynamics. However, data from many plots have not been analyzed and empirical growth and yield models are not widely available. Although, some encouraging efforts have been made to develop growth prediction models, most of them have not been implemented for practical application (Yong 1998). There is an urgent need to exploit the massive amount of data available and develop a robust quantitative growth prediction system that could be calibrated for different forest sites in Peninsular Malaysia.

Several emerging challenges to Malaysian forestry require the development of quantitative growth models. Malaysia is one of the signatories of the ITTOⁱ

Objectives Year 2000, which requires Malaysia to improve management of its forest to allow it to market its timber internationally as wood harvested from sustainably managed forests. As a producer member country of ITTO, Malaysia is fully committed to achieving sustainable forest management in the overall context of sustainable development (Thang 2000). Presently, Malaysia implements strong sustainability measures in its forest management based on ITTO guidelines. Furthermore, introduction of reduced impact logging methods to the management of dipterocarp forest provides a wider opportunity to control the quality of future growing stock through silvicultural manipulation. Informed selection harvesting design and intensity should be an integral part of sustainable forestry (ITTO 1992; Chin et al. 1996). Development of a quantitative growth model and application of density indices to assessing growing stock would improve precision for exploring the impact of management options and silvicultural alternatives on second growth dipterocarp forest. This thesis is divided into three key chapters to address three respective objectives:

- a) Test the hypothesis that a maximum size-density relationship can be identified in hill dipterocarp forests;
- b) Develop growth equations to predict annual diameter or basal area increment from initial stand structure and tree conditions;
- c) Develop guidelines for applying the maximum size-density concept to growing stock assessment and control in hill dipterocarp forest.

Table 1: Silvicultural practices in Peninsular Malaysia

Period	Silvicultural practices
1910-1926	Malayan Improvement Felling -aimed at improving the existing timber crop for future exploitation by series of felling; pole felling, seeding felling, and final felling -it is treatment or tending operation and not regeneration operation -treatment done by releasing of larger advanced regeneration from the competition of less valuable trees
1926-1942	Malayan Regeneration Improvement System -aimed at breaking canopy cover to allow regeneration establishment -the system involve several series of girdling before commencement of final felling to assist the establishment desired regeneration
1945 – mid-1960's	Malayan Uniform System -a system for converting virgin tropical rainforest to more or less even-aged forest containing a greater proportion of economically valuable species. -achieved by one felling of commercial trees greater than 45 cm dbh and of selected natural regeneration of varying age, aided by systematic poison-girdling of unwanted species. -success of the system depended on the presence of seedling regeneration of the commercial species on the ground at the time of harvesting
mid-1960's-1970's	Modified Malayan Uniform System -similar to MUS except for several variations due to changing demand of forest industry -retention of advanced growth of potentially commercial species -adequate regeneration stocking is not mandatory
1978 onwards	Selective Management System -designed to optimize management objectives that include economically efficient harvesting, sustainability of the forest, and minimum forest development cost. -requires selection of management regime based on inventory data, and equitability both to the logger and to the forest owner, as well as ensuring ecological integrity and environment quality -sequence of operations consists of pre-felling inventory, marking of trees for felling, and post felling inventory to determine the appropriate silvicultural treatments -success depends on the growth and mortality rates of residual trees, reducing logging damage, and adequate stocking of healthy residual trees

(Sources: Wyatt-Smith, 1963; Thang, 1987)

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CHAPTER 2

EVALUATION OF THE MAXIMUM SIZE-DENSITY RELATIONSHIP IN PRIMARY HILL DIPTEROCARP FORESTS OF PENINSULAR MALAYSIA

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EVALUATION OF THE MAXIMUM SIZE-DENSITY RELATIONSHIP IN PRIMARY HILL DIPTEROCARP FORESTS OF PENINSULAR MALAYSIA

ABSTRACT

Data from temporary and permanent sample plots in mixed dipterocarp forest of Peninsular Malaysia were examined to test the applicability of the maximum size-density concept. Regression analysis was used to select the appropriate power, k , on tree dbh for relating maximum size-density to stand structure. Two types of structural parameters were tested: skewness and variance of dbh^m . Different community types were also tested using the extra sum-of-squares F-test to determine its correlation with size-density relation. Regression analysis indicated that maximum size-density is affected by stand structure but weakly correlated with community. The larger spatial scale showed a more stable $\ln(Dq) \sim \ln(\text{tph})$ combination closed to the maximum size-density trajectory of Bukit Lagong plot. Considerably larger scale is more appropriate to examined maximum size-density limit for uneven-aged, mixed species forest. Findings from two long-term permanent sample plots in primary mixed dipterocarp forest indicated that the maximum size-density limit is quite consistent. Several stand trajectories deviated from the limit for short periods, but returned to the same limit after a few years. The deviation of the stands and their eventual return reflected tree recruitment and residual growth following release of growing space after individual tree mortality. The recommended slope for a working model in the hill dipterocarp forest following the geometric mean regression (GMR) approach is 2.61.

Key words: maximum size-density, structural parameters, size-density trajectory, spatial scale

INTRODUCTION

The maximum size-density concept has been fundamental to the practice of silviculture in temperate regions for several decades (Long and Daniel 1990). This concept helps the silviculturist to design and implement strategies for achieving a wide range in stand structural objectives and desired species composition. Appropriate silvicultural strategies involving stand density manipulation require considerable insight into future stand development, especially the competitive effects depicted in stand density management diagrams at both the tree and stand level (Drew and Flewelling 1977, 1979). One strategy is to allocate growing stock based on the maximum carrying capacity of the stand as measured by stand density index (Long and Daniel 1990; Cochran 1992).

Stand density index quantifies the level of inter-tree competition in pure even-aged stands regardless of stand age and site quality and hence, it provides one way to quantify the maximum size-density limit. In theory, stands approach their size-density limit as they grow over time in that this limit defines a maximum average size that trees can attain at a given number of trees per unit area (Reineke 1933; Yoda et al. 1963; Drew and Flewelling 1977, 1979; Hann and Wang 1990). Further increases in tree size can only be gained by release of growing space through mortality of some of the existing trees.

Stand density index was first introduced into the forestry literature by Reineke (1933) with the objective of standardizing the number of trees per unit area and average size of trees in a given stand to a competitively equivalent number of trees with average diameter of 25 cm. Yoda et al. (1963) introduced a concept known as the $-3/2$ power law of self-thinning, which dealt more directly with the concept that stands approach a maximum size-density limit over time. The law was based on pure even-aged stands of plants in which the slope of the logarithm of mean size plotted on logarithm of mean number per unit area was $-3/2$. The

theoretical value of $-3/2$ for the slope followed from the assumption that the horizontal space occupied by a plant is proportional to the square of some linear dimension (for example diameter), and that mass is proportional to the cube of the same linear dimension. Drew and Flewelling (1977,1979) extended the $-3/2$ law to forestry by relating the number of trees to average stem volume. Their demonstrated applications pertained to pure, even-aged populations. More recently, Kikuzawa (1999) examined the relationship between mean plant size, size distribution, and self-thinning under one-sided competition in pine and birch forests. He suggested that the competition among individuals determined the size-density limits among stands, which in turn determines the size structure of the stand.

Although the maximum size-density concept originated from observations in pure even-aged stands of herbaceous plants and trees, this concept has been expanded to uneven-aged stands of trees (Long and Daniel 1990; Cochran 1992), as well as uneven-aged, mixed-species forests stands (Sterba and Monserud 1993). Extension to uneven-aged stands must take into account the variability in stand structure and species mixture. Sterba and Monserud (1993) examined the influence of stand structure and habitat type on the slope of the maximum size-density line. They found that the slope depended on skewness of the $\text{dbh}^{1.5}$ distribution, which is correlated with stand structural characteristics such as variability in stand age and species mixture. Uneven-aged stands with highly skewed, reverse J-shaped diameter distributions have a nearly vertical maximum size-density line when log of mean dbh is plotted on log of mean trees per hectare. Tropical rainforests, which are extremely uneven-aged and mixed in species composition, seem to exhibit a maximum and constant basal area; for example, Manokaran (1998) found that stand basal area of primary lowland dipterocarp forest and a regenerating lowland dipterocarp forest was quite similar, although both stands had marked differences in stand structure and tree density. In the regenerating forests, the scarcity of larger trees was compensated for by large number of small trees. Long-term studies in

two ecological plots have also shown movement towards equilibrium with respect to basal area (Manokaran and Swaine 1994); basal area maintained a steady state over a period of approximately 37 years, although the number of trees decreased by 14 percent. It was suggested that loss of trees to mortality was offset by the incremental growth of the surviving trees and recruitment of new trees, which grew above the minimum measured diameter. If the maximum size-density limit is a fixed basal area, the slope on the $\ln(Dq) \sim \ln(\text{tph})$ line is implied to be -2 . It is interesting to note that this slope would be consistent with the assumption behind the theoretical value of $-3/2$ law, if in fact the average total mass on stem volume of a tree is proportional to Dq^3 .

A stand at its maximum size-density line has reached the maximum carrying capacity for the site. Allowing the stand to remain at this high relative density would hinder individual tree development to some degree, depending on the level of differentiation. Forest managers typically select a lower relative density to ensure good growth of the residual trees. For example, the desired managed stand density of temperate forests has been suggested to be as high as 66 % of the biological maximum density (Cochran 1992) or as low as 55 % (Drew and Flewelling 1977).

The maximum density line can guide allocation of growing stock to various strata in mixed hill dipterocarp forest in a manner similar to uneven-aged stands in the temperate zones (Long and Daniel, 1990; Cochran 1992). High density in the overstory reduces growing space for understory trees. Allocation of growing stock determines the trees in specific size classes to be removed and retained during harvest. The growth response to a given allocation of growing stock will depend both on the residual stand structure and on the accuracy of estimating maximum carrying capacity of the site.

The objectives of this study were:

- a) to test for the existence of a size-density limit in primary hill dipterocarp forest based on large number of temporary plots,
- b) to test if this limit varies by stand structure (size class distribution) and species composition, and
- c) to test the hypothesis that stand developmental patterns displayed by permanent plots in primary dipterocarp forests support the existence of a maximum size-density limit.
- d) to test the importance of spatial scale in defining a stable maximum size-density limit vs. a limit that varies by stand structure

Stand development in tropical forests is quite rapid relative to most temperate forests; hence, observing stand development over a 48-year period would be equivalent to observing over a period several times as long in most temperate systems. Also, the permanent plots available for analysis were quite large. We therefore hypothesized stand trajectories for these permanent plots will diverge from the maximum line when mortality of trees occurs and will begin to approach the maximum again after mortality promotes ingrowth of small trees and growth of surviving trees around the resulting gaps.

MATERIAL AND METHODS

Source of Data

Two types of data were taken from primary dipterocarp forest in Peninsular Malaysia (Table 2, Figure 1). Single-measurement (temporary plot) data were used to identify a general maximum size-density equation, and to test the effects of stand structure and species composition. Repeated-measure data allowed analysis of successive position by size-density coordinates for all tree species combined. In

other words, size-density trajectories could be graphed on stand density diagrams to validate or refute the maximum size-density line inferred from the temporary plot data.

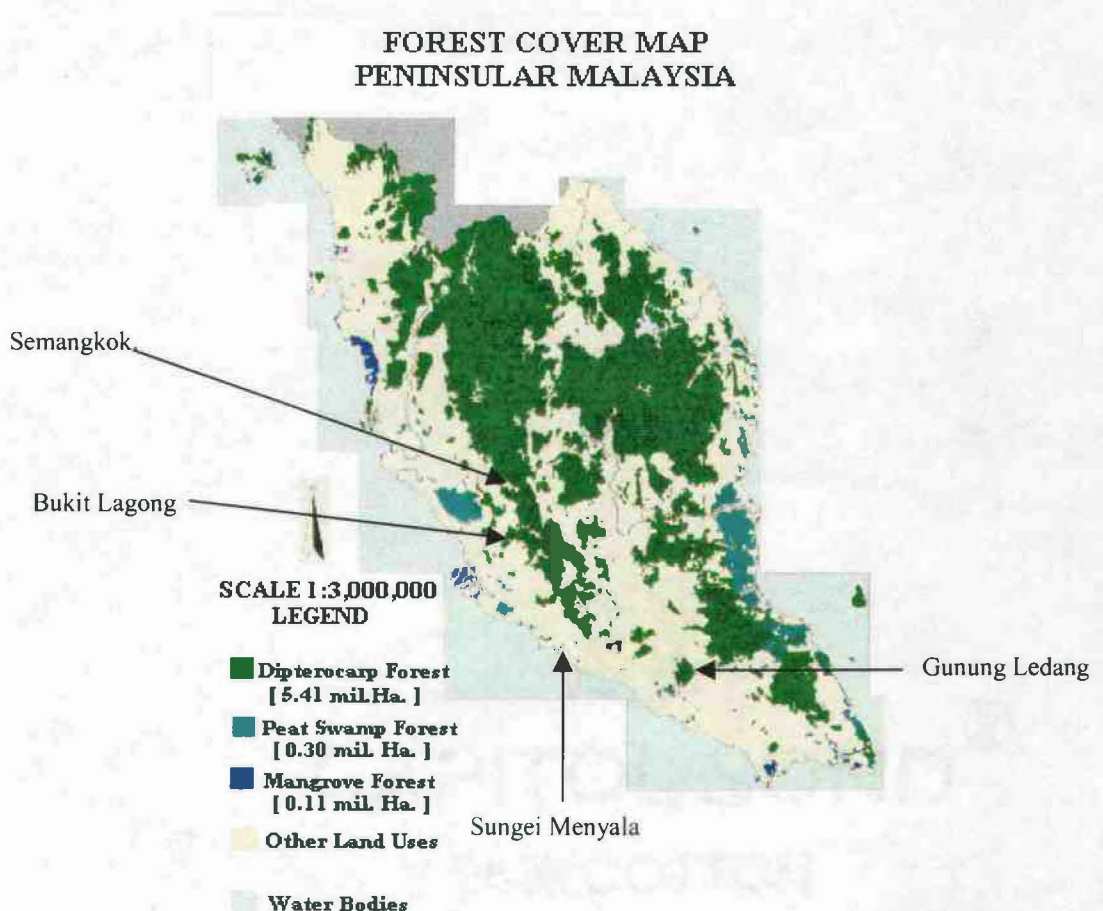
Single-Measure Data

Two sets of single-measure data were selected for the analysis: a) a contiguous six hectare ecological plot; and b) a ten percent systematic line-plot inventory. The 6-ha contiguous plot (200 m x 300 m) is located at Semangkok Forest Reserve (Figure 1). The forest is classified as Seraya-Ridge Forest due to the predominance of *Shorea curtisii* on the ridges. Each plot is subdivided to 150, 400-m² (20 m x 20 m) quadrats, and further subdivided to four 100 m² quadrat within the 400-m² quadrats (Table 3a). All trees with dbh \geq 5 cm were identified to species and dbh was measured by diameter tape to the nearest 0.1 cm.

The inventory line-plot is located in a virgin jungle reserve at Gunung Ledang Forest Reserve (Figure 1). The forest can be classified as mixed hill dipterocarp forest. Predominance of Seraya (*Shorea curtisii*) can be seen on the ridges. The aim of the inventory was to gather information on growing stock by species composition and size structure from large trees down to seedlings. In the analysis of maximum density limits, only trees with dbh $>$ 5 cm dbh were considered. All trees with dbh \geq 5 cm were measured to the nearest 0.1 cm and species identification was determined by vernacular names. The sampling intensity of the systematic line-plot varies with size of trees. Distance between the inventory lines was 100 m, except for the first line, which is 50 m from the starting point. The main plot was 50 m x 20 m for trees with dbh \geq 30 cm. Distance between plots was also 100 m. Within each main plot, there were three sub-plots varying in size in according to tree dbh class (Table 3b). For the purpose of maximum size-density

analysis, all plots data were expanded to trees per hectare. The total number of plots available from Gunung Ledang was 529.

Figure 1: Forest map and location of study site



Repeated-Measures Data

The repeated-measure data were taken from two long-term permanent ecological plots. The plots are located in a lowland dipterocarp forest at Sungei Menyala Forest Reserve and a hill dipterocarp forest at Bukit Lagong Forest Reserve (Figure 1). At both sites, a plot of five acres, or 10 x 5 chains (201.2 m x

100.6 m) was established (Manokaran and Swaine, 1994). Five quadrats at Sungei Menyala and five quadrats at Bukit Lagong had been disturbed in 1917 and 1913, respectively (Wyatt-Smith, 1966). The Sungei Menyala plot was established in 1947, while the Bukit Lagong plot was established in 1949. All subsequent 21 re-measurements were done in the same years for both plots (Appendix 1a and 1b). Stand attributes varied between plots and between years within plots (Table 4).

Identification of the Maximum Size-Density Line

The basic model form of the maximum size-density equation was as follows:

$$\ln(Dq) = a_0 + a_1 \ln(tph) \quad [1]$$

where,

Dq = estimated quadratic mean diameter

tph = trees per hectare

a_0 and a_1 = parameters estimated from the data

This basic model was fitted to both the Semangkok and Gunung Ledang data to obtain initial insight into the average slope of the maximum size-density line.

Table 1: Study site descriptions. Data on Bukit Lagong and Sungei Menyala represent 1971 measurements described by Manokaran and Swaine (1994). Semangkok data were collected in 1977 and Gunung Ledang data in 1999

Location (Forest Reserve)	Forest Types	Five most common species	Stocking all trees		Elevation (m)	Annual Rainfall (mm)
			tph (no/ha)	BA (m ² /ha)		
<i>Permanent plots</i>						
Bukit Lagong	HDF	<i>Hynocarpus filipes</i> ^b <i>Scaphium macropodum</i> ^b <i>Shorea laevis</i> ^a <i>Pentace strychnoidea</i> ^b <i>Anisophyllea corneri</i> ^c	494.0	41.11	460-550	2481
<i>Temporary plots</i>						
Sungei Menyala	LDF	<i>Santiria laevigata</i> ^b <i>Ixonanthes icosandra</i> ^b <i>Porterandia anisophylla</i> ^c <i>Shorea parvifolia</i> ^a <i>Trigoniasrum hypoleucum</i> ^b	476.5	31.81	30	2286
Semangkok	HDF	<i>Shorea curtisii</i> ^a , <i>Lithocarpus wallichianus</i> ^b <i>Teijsmanniodendron coriace</i> <i>Scaphium macropodum</i> ^b <i>Antidesma cuspidatum</i>	493.3	42.67	340-450	2414
Gunung Ledang	HDF	<i>Shorea curtisii</i> ^a <i>Scaphium macropodum</i> ^b <i>Alstonia augustiloba</i> ^a	471	35.5	350-750	2100

* HDF: Hill dipterocarp forest, LDF: Lowland dipterocarp forest, Ecological groups (a: emergent b: main canopy c: understorey) tph: trees per hectare, BA: basal area per hectare

Table 3: Size and number of plots used for developing and validating maximum size-density limits

(a) Contiguous plot data, Semangkok

Plot dimension	Subplot dimension	Area (m ²)	Area (ha)	Number of plots
200m x 300 m	20 m x 20 m	400	0.04	150

(b) Nested inventory plot data, Gunung Ledang

Nested plot dimensions	Area (m ²)	Area (ha)	Sampling intensity (%)	Dbh class (cm)	Expansion factor
50 m x 20 m	1000	0.10	10	+30	10
25 m x 20 m	500	0.05	5	15 – 30	20
10 m x 10 m	100	0.01	1	5 – 15	100

Table 4: Summary stands statistics for Bukit Lagong and Sungei Menyala: quadratic mean dbh, trees per hectare, periodic mortality and ingrowth as average of twenty-one re-measurements

Variables	Bukit Lagong F.R.			Sungei Menyala F. R.		
	Minimum	Mean	Maximum	Minimum	Mean	Maximum
Dq	31.4	33.2	34.8	28.0	29.4	31.1
tph	430	490	548	440	480	537
BA	40.1	43.8	43.8	30.6	32.7	33.6
<u>Mortality</u>						
Dq	24.2	32.4	48.1	18.1	25.0	32.8
tph	6.5	14.0	25.5	10.0	19.5	38.0
BA	0.32	1.30	2.27	0.34	1.04	2.08
<u>Ingrowth</u>						
Dq	10.4	11.0	14.7	10.4	11.0	14.5
tph	2.0	9.45	26.0	1.5	14.0	35.5
BA	0.03	0.10	0.29	0.02	0.13	0.32

Dq= quadratic mean diameter is calculated

tph= Trees per hectare

BA=Total tree basal area

The maximum size-density limit of hill dipterocarp forests was hypothesized to be a function of stand structure, specifically the skewness and variance of the diameter distributions. Four transformations of tree dbh were investigated, all of which took the form dbh^m , where $m = 1, 1.5, 2$ and 2.5 (based on Sterba and Monserud 1993). In the basic model above, hypotheses about stand structural effects were tested by allowing the parameters a_0 and a_1 to vary as a function of variance and skewness of the transformed diameters.

The mean and range of the skewness and variance for Semangkok contiguous plots and Gunung Ledang nested inventory plots are shown in Table 5 and Table 6, respectively. To gain an initial assessment of the relative performance of different transformations of dbh, the following general model form was fitted:

$$\ln(Dq) = c_0 + c_1 f_j(\text{dbh}^m) + c_2 \ln(\text{tph}) + c_3 f_j(\text{dbh}^m) \ln(\text{tph})$$

or

$$\ln(Dq) = [c_0 + c_1 f_j(\text{dbh}^m)] + [c_2 + c_3 f_j(\text{dbh}^m)] \ln(\text{tph}) \quad [2]$$

where $f_1(\text{dbh}^m) = 0$

$$f_2(\text{dbh}^m) = s_m^2$$

$$f_3(\text{dbh}^m) = \text{sk}_m$$

The three functions of dbh^m and 4 values of m led to 12 possible models for comparison.

Hence, the general model was expanded to:

$$\begin{aligned} \ln(Dq) = & (a_1 + a_2 s_{1.0}^2 + a_3 s_{1.5}^2 + a_4 s_{2.0}^2 + a_5 s_{2.5}^2 + a_6 \text{sk}_{1.0} + a_7 \text{sk}_{1.5} + a_8 \text{sk}_{2.0} + a_9 \text{sk}_{2.5}) \\ & (b_1 + b_2 s_{1.0}^2 + b_3 s_{1.5}^2 + b_4 s_{2.0}^2 + b_5 s_{2.5}^2 + b_6 \text{sk}_{1.0} + b_7 \text{sk}_{1.5} + b_8 \text{sk}_{2.0} + b_9 \text{sk}_{2.5}) \ln(\text{tph}) \end{aligned} \quad [3]$$

where s_m^2 = sample variance for dbh^m

sk_m = sample skewness for dbh^m

$$= (n/(n-1)(n-2)) ((dbh^m - DBH^m)/s)^3$$

where dbh_i^m = dbh^m of i th tree

DBH^m = mean dbh^m for the plot

$a_1, a_2, a_3, a_4, a_5, a_6, a_7, a_8, a_9, b_1, b_2, b_3, b_4, b_5, b_6, b_7, b_8, b_9$ are parameters estimated from the data.

Exploration for a full model was conducted by all-subsets regression analysis, allowing any combinations of skewness and variance of dbh^m to enter the model. The two best subsets of variables from each model size were further examined. Each selected subset of predictor variables included at least the natural logarithm of trees per hectare, or the interaction of the natural logarithm of trees per hectare with other predictors. The criteria applied for selecting the best fit included Mallows C_p , adjusted R^2 and Furnival Index (Furnival 1961). Using the C_p statistics, the best model is considered when C_p value is lowest and equal to or close to the number of parameters estimated in the model. Using the adjusted R^2 , the best model is that producing the highest R^2 value and the least number of variables. A model with this characteristic would have a small mean square error, and when the C_p statistic approximately equals the number of parameters, the lack of fit is also small (Draper and Smith 1981). Preferred models should also be simple while retaining relationships important for explaining silvicultural or biological mechanisms of the system.

Table 5: Means and ranges of variables tested in the maximum size-density equation for Semangkok contiguous plots

Variables	Minimum	Mean	Maximum
Response:			
Dq	17.0	31.4	70.1
Predictors:			
tph	125	490	850
sk = sk(dbh ¹)	0.103	1.860	4.070
ska = sk(dbh ^{1.5})	0.215	2.280	4.800
skb = sk(dbh ^{2.0})	0.314	2.610	5.200
skc = sk(dbh ^{2.5})	0.397	2.860	5.400
s ² = s ² (dbh ¹)	24.7	402	2430
s ² a = s ² (dbh ^{1.5})	983	47400	5.50*10 ⁵
s ² b = s ² (dbh ^{2.0})	3.18*10 ⁴	5.72*10 ⁶	1.20*10 ⁸
s ² c = s ² (dbh ^{2.5})	9.29*10 ⁵	7.56*10 ⁹	2.61*10 ¹⁰

Dq: Quadratic mean diameter, tph: trees per hectare

Table 6: Means and ranges of variables tested in the maximum size-density equation for Gunung Ledang nested inventory plots

Variables	Minimum	Mean	Maximum
Response:			
Dq	20.0	31.1	60.1
Predictors:			
tph	80	472	1270
sk = sk(dbh ¹)	0.31	1.99	4.89
ska = sk(dbh ^{1.5})	0.577	2.610	6.45
skb = sk(dbh ^{2.0})	0.815	3.170	7.66
skc = sk(dbh ^{2.5})	1.02	3.640	8.66
s ² = s ² (dbh ¹)	18.9	312	1270
s ² a = s ² (dbh ^{1.5})	1000	31900	2.04*10 ⁵
s ² b = s ² (dbh ^{2.0})	42900	3.18*10 ⁶	3.31*10 ⁶
s ² c = s ² (dbh ^{2.5})	1.65*10 ⁶	3.37*10 ⁸	4.4*10 ⁹

Dq: Quadratic mean dbh

tph: Trees per hectare

In addition to the influence of stand structure, parameters of the size-density model may vary by species composition or community type. A community type classification was previously identified by hierarchical cluster analysis using PC-ORD multivariate statistical software (McCune and Medford 1995). Five levels of community types were identified for Semangkok and three for Gunung Ledang. Possible classifications included two, three, four, five or six community groups for Semangkok (Table 7), and two, three or four community groups for Gunung Ledang (Table 8).

Model [1] was modified by introducing indicator variables for community types. Separate models were fit for the alternative community typing at each site. For example, the model assuming three community groups was:

$$\ln(D_q) = d_0 + d_1cg2 + d_2cg3 + (e_0 + e_1cg2 + e_2cg3) \ln(tph) \quad [4]$$

$$\text{where } cg2 = \begin{cases} 1 & \text{if community type 2} \\ 0 & \text{otherwise} \end{cases}$$

$$cg3 = \begin{cases} 1 & \text{if community type 3} \\ 0 & \text{otherwise} \end{cases}$$

Extra sum-of-squares tests were applied to determine the statistical significance of community type on the maximum size-density line. If the inclusion of community structure type led to significant improvement in predicting $\ln(D_q)$, then it was incorporated into the selected model with the structural parameters as predictors. The final model was selected based on the rmse, R^2 and significance level of the predictors.

Table 7: Number of plots in each community type at Semangkok

Number of clusters	Community type					
	1	2	3	4	5	6
Two	73	77				
Three	73	53	24			
Four	48	53	24	25		
Five	48	27	24	25	26	
Six	28	27	24	25	26	20

Table 8: Number of plots in each community type at Gunung Ledang

Number of clusters	Community type			
	1	2	3	4
Two	293	232		
Three	220	232	73	
Four	220	141	73	91

Identification of Maximum Density Line Based on Repeated Measures Data

We analysed the maximum density line based on repeated measures data of Bukit Lagong plot using two regression method (1) ordinary least square, and (2) geometric mean regression (GMR). The ordinary least square method was to test the hypothesis that maximum size-density slope differs from the hypothesized values of 1.605 (Reineke 1933) and 2.0 (Manokaran and Swaine, 1995). The maximum size-density slope of 2.0 implied a constant basal area. The basic model was fit by regressing $\ln(\text{tph})$ on $\ln(\text{Dq})$. We adopted the geometric mean regression (GMR) method (Ricker 1984) that determines the central trend lines to avoid the potential controversy as to whether Dq should be regressed on tph , or tph on Dq . Our aim was to establish a maximum size-density slope that could be

recommended as a working model for hill dipterocarp forest. In its simplest form, the slope of the GMR of variable Y on X is equivalent to the ratio of the standard deviations or the dispersions of the two sets of observations:

$$s_y/s_x = (\sum y^2 / \sum x^2)^{0.5}$$

where $y = Y - \text{mean}(Y)$, Y is $\ln(Dq)$
 $x = X - \text{mean}(X)$, X is $\ln(\text{tph})$

Maximum Size-Density Trajectories from Long-Term Plots

The long-term trajectory across size-density coordinates was examined for the 2-ha plot of Sungei Menyala and Bukit Lagong by examining successive locations on a stand density management diagram ($\ln(Dq) \sim \ln(\text{tph})$), and by plotting periodic changes in Dq, mortality, ingrowth, skewness and variance of the dbh distributions. Scatter matrix plots of these variables were also produced to help interpret general trends in stand dynamics for the two plots (Appendix 2).

The long term stand trajectory of Bukit Lagong and Sungei Menyala plots were plotted on a stand density diagram resulting from parameter estimates in model [3].

$$\ln(Dq) = b_0 + b_1 \ln(\text{tph})$$

$$Dq = \exp(b_0) \text{tph}^{b_1}$$

$$\exp(-b_0) Dq = \text{tph}^{b_1}$$

$$\exp(b_0/b_1) Dq^{-1/b_1} = \text{tph}$$

$$\exp(-b_0/b_1)/25.4^{-1/b} = \text{tph} (Dq^{-1/b_1})/ 25.4^{-1/b}$$

$$\text{sdi} = \text{tph} (Dq/25.4)^{-1/b}$$

where b_0 is the intercept term and b_1 is the slope of the size-density equation derive from structural parameters identified in model [3]

Influence of Spatial Scale on Size-Density Limits

The influence of spatial scale on the size-density limits was examined using the contiguous 6-ha plot of Bukit Lagong plot. Defining the limit as a function of stand structure on relatively small plots could be complicated due to the edge effects and local variations typical of mixed uneven-aged stands. Death of large trees or groups of trees create gaps in which other trees grow. These trees reach maturity and eventually senesce and die. Forest structure is continually changing as mortality and recruitment of new trees occurs (Whitmore 1984). It is hypothesized that local variation is higher for smaller plots than larger ones, particularly as plot size approaches the canopy size of dying groups or individuals. Niiyama (1999) reported that 15.6 percent of Semangkok 6-ha plot is classified as canopy gap with height <10 m. The presence of bamboo on the lower slope and abundance of *Eugeissona triste* palms on the ridges and upper slope in the understorey also affect the local variation in stand structure. We examined the $\ln(Dq) \sim \ln(tph)$ scatter points of contiguous plots within the 6-ha plot in Semangkok at six different spatial scales (Table 9), hypothesizing that spatial scale affects assessment of the maximum size-density limit in primary hill dipterocarp forest.

Table 9: Contiguous plots at six spatial scale within Semangkok 6-ha plot

Plot size (m ²)	Number of plots
400	150
800	75
1200	50
2400	25
10000	6
20000	3

RESULTS AND DISCUSSION

Maximum Size-Density limits for Primary Hill Dipterocarp Forest

Semangkok Contiguous Plot

When considering the different transformations on dbh in model [2], the best predictive power was obtained from $\text{dbh}^{1.0}$, that is, the lowest rmse and the highest R^2 values were obtained under no transformation of dbh (Table 10). Stand skewness or variance of the diameter distribution improved the fit of the maximum size-density equation. However, for each dbh transformation the variance yielded a better model than skewness. The basic model only explained 3 % of the variation in $\ln(Dq)$, whereas the model with a single interaction of variance with $\ln(\text{tph})$ increased R^2 to 76%.

Table 10: Results of regression analysis with $\ln(Dq)$ as dependent variables and $\ln(tph)$ with stand skewness and variance, model [2] for Semangkok contiguous plots (N=150)

Models	Variables	R^2	rmse
	$\ln(Dq) = a_0 + a_1 \ln(tph)$	0.03	0.25
1	$sk(dbh^1)^{ns}, sk(dbh^1):tph^{ns}, tph^{ns}$	0.09	0.25
2	$sk(dbh^{1.5})^{ns}, sk(dbh^{1.5}):tph^{ns}, tph^{ns}$	0.11	0.25
3	$sk(dbh^2)^{ns}, sk(dbh^2):tph^{ns}, tph^{ns}$	0.11	0.24
4	$sk(dbh^{2.5})^{ns}, sk(dbh^{2.5}):tph^{ns}, tph^{ns}$	0.12	0.24
5	$s^2(dbh^1)^{ns}, s^2(dbh^1):tph^{ns}, tph$	0.76	0.13
6	$s^2(dbh^{1.5}), s^2(dbh^{1.5}):tph^{ns}, tph$	0.60	0.13
7	$s^2(dbh^2), s^2(dbh^2):tph, tph$	0.47	0.19
8	$s^2(dbh^{2.5}), s^2(dbh^{2.5}):tph, tph$	0.38	0.20

rmse is residual mean square error, n.s. : not significant

The combination of s^2a and s^2 in model [3] improved the fit to explain 89 % of the total variation in $\ln(Dq)$ (Table 11). Predictability of model stabilized when the number of predictor variables was greater than three. The selected model included s^2a and s^2 . Residual analysis revealed a serious lack of fit over s^2a , so this variable was transformed to its natural logarithm. The selected model for the Semangkok data was:

$$\ln(Dq) = 1.66 + 0.17 \cdot \ln(s^2a) + 0.000022(s^2) \cdot \ln(tph) \quad [5]$$

The resulting R^2 and rmse were 0.89 and 0.083, respectively. Both the intercept term and slope of equation [5] were positively related to variance of $dbh^{1.5}$ distribution and variance of dbh distribution, respectively (Figure 2 & 3). The effect of the variance of dbh distribution on the slope was not obvious (Figure 4).

Extra-sum of square tests on the statistical significance of community type indicated lack of any predictive power for plot classifications with five or six types (Table 12); that is, no community types had any influence on the slope or intercept of the model. The scatter plot of natural logarithm of both tree density and

quadratic mean dbh of all community types is shown in Figure 5a-f. In general, the results indicated that the community type has no strong influence on the maximum size-density limit. Apparently, community type and structural parameters of the dbh distribution were weakly correlated.

Table 11: Results of all-subset regression analysis of model [3] using structural parameters (skewness and variance) of dbh raised to varying powers as predictors for Semangkok contiguous plots

Variables	Cp	p	R ²	rmse	FI
(tph)	480.9	2	75	0.130	4.07
s ² a(tph)	931.4	2	56	0.170	5.30
s ² a,s ² (tph)	128.5	3	89	0.090	2.82
s ² (tph),s ² a(tph)	157.7	3	88	0.091	2.85
s ² a,s ² c,s ² (tph)	109.8	4	90	0.083	2.60
sk,s ² a,s ² (tph)	110.2	4	90	0.083	2.60
s ² a,s ² c,s ² (tph),sk(tph)	95.0	5	92	0.080	2.51
sk,s ² a,s ² c,s ² (tph)	95.3	5	91	0.081	2.54
ska,s ² a,s ² c,s ² (tph),sk(tph)	56.9	6	92	0.074	2.32
s ² a,s ² c,s ² (tph),sk(tph),ska(tph)	61.9	6	92	0.074	2.32
sk,ska,s ² a,s ² c,s ² (tph),sk(tph)	56.1	7	93	0.073	2.29
ska,s ² a,s ² c,s ² (tph),sk(tph),ska(tph) ^{ns}	56.5	7	93	0.073	2.29
sk,ska,skb,skc,s ² a,s ² c(tph)	10.5	8	94	0.077	2.41
sk,ska,skb,skc,s ² a,s ² c ^{ns}	15.4	8	94	0.065	2.04
sk,ska,skb,skc,s ² a,s ² c ^{ns} ,s ² c(tph)	9.2	9	94	0.063	1.98
sk,ska,skb,skc,s ² a,s ² c(tph) ^{ns} ,s ² c(tph)	10.6	9	94	0.064	2.01
sk,ska,skb,skc,s ² a,s ² c,s ² c(tph),sk(tph) ^{ns}	10.4	10	94	0.063	1.98
sk,ska,skb,skc,s ² a,s ² c ^{ns} ,s ² c(tph),skc(tph) ^{ns}	10.6	10	94	0.063	1.98

"ns" not significant at 5% probability level

p is the number of co-variates in the model

tph is ln(tph)

Explanation for sk,ska,skb,skc, s²a,s²b and s²c is given in Table 5.

Although the variance of dbh distributions improved the model fit significantly, the parameter estimate did not exhibit the expected sign for maximum size-density equation, i.e., the slope parameter was non-negative. The model is apparently invalid for estimating the stand density index for the hill dipterocarp forest.

Table 12: Summary results of extra sums of squares tests on the effect of community type on the maximum size-density line (model [4]) for Semangkok contiguous plots (N=150)

Number of clusters		coefficient for k =						ESS F-test (P-value)
		0	1	2	3	4	5	
Two	d_k	3.142	0.0143 ^{ns}					0.017
	e_k	0.090 ^{ns}	-0.028 ^{ns}					
Three	d_k	3.014	0.157 ^{ns}	-0.114 ^{ns}				0.0241
	e_k	0.129 ^{ns}	-0.024 ^{ns}	0.043 ^{ns}				
Four	d_k	3.183	0.169 ^{ns}	0.175 ^{ns}	-0.132 ^{ns}			0.0322
	e_k	0.082 ^{ns}	-0.033 ^{ns}	-0.040 ^{ns}	0.044 ^{ns}			
Five	d_k	3.166	0.169 ^{ns}	0.175 ^{ns}	-0.024 ^{ns}	-0.125 ^{ns}		0.0486
	e_k	0.083 ^{ns}	-0.033 ^{ns}	-0.040 ^{ns}	0.008 ^{ns}	0.037 ^{ns}		
Six	d_k	3.196	0.093 ^{ns}	0.146 ^{ns}	0.114 ^{ns}	-0.021 ^{ns}	-0.106 ^{ns}	0.1100
	e_k	0.074 ^{ns}	-0.06 ^{ns}	-0.041 ^{ns}	-0.026 ^{ns}	0.007 ^{ns}	0.031 ^{ns}	

“ns” indicates non-significant predictor with P-value<0.05. ESS is the extra sum of squares for the F-test.

Figure 2: The relationship between the intercept of the maximum size-density line and the variance of the $\text{dbh}^{1.5}$ distribution at Semangkok

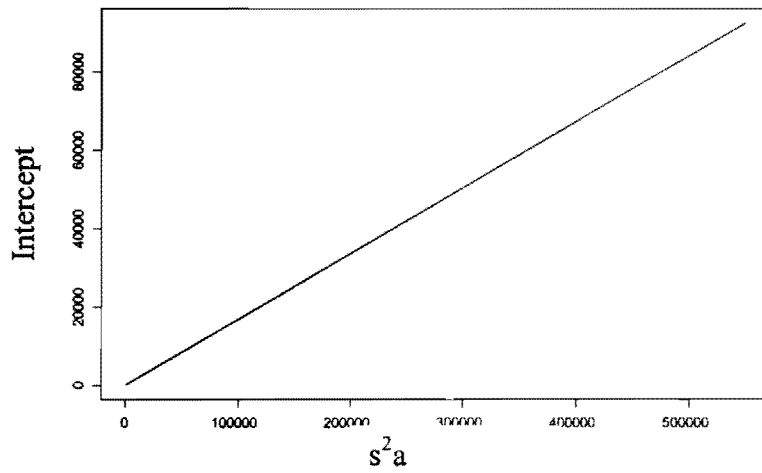


Figure 3: The relationship between the slope of the maximum size-density line and the variance of the dbh distribution at Semangkok

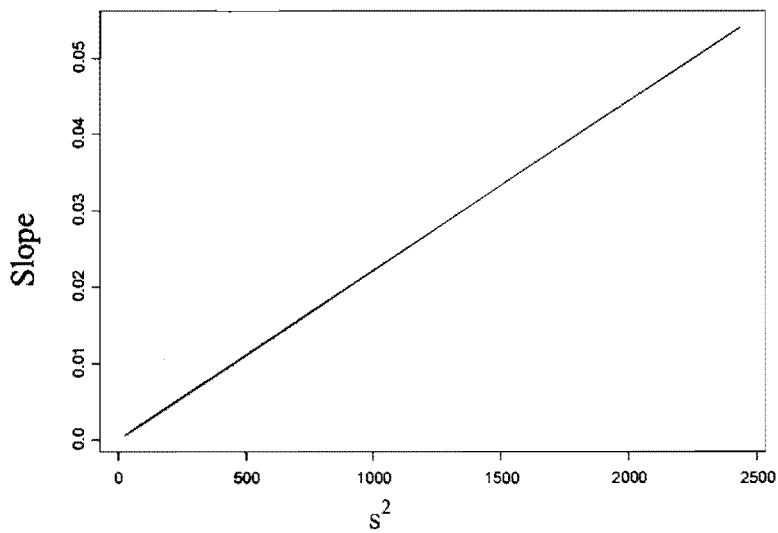


Figure 4: The maximum size-density slope for Semangkok from equation [5] and under four conditions; a) $\max s^2$, $\max s^2 a$; b) $\min s^2$, $\max s^2 a$; c) $\max s^2$, $\min s^2 a$; and d) $\min s^2$, $\min s^2 a$

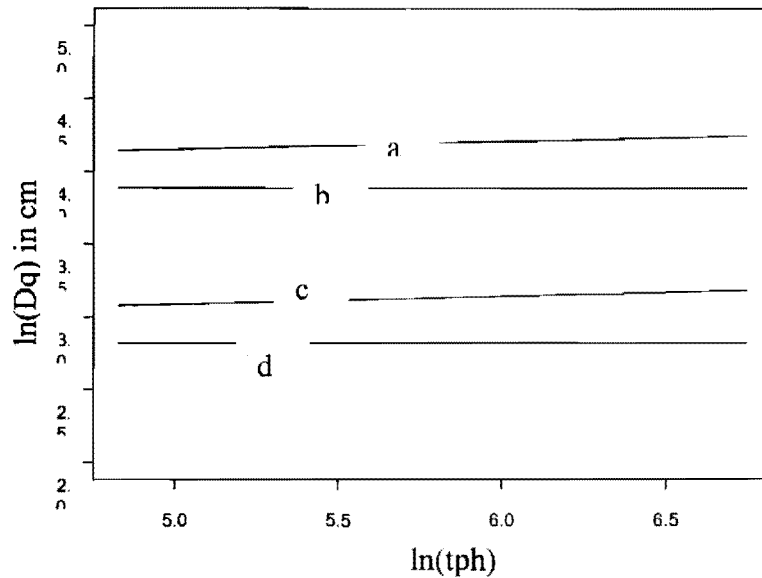
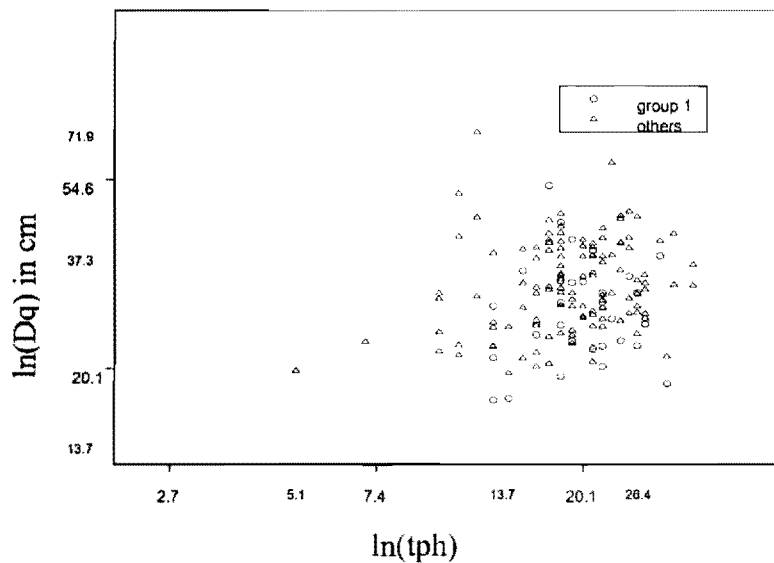
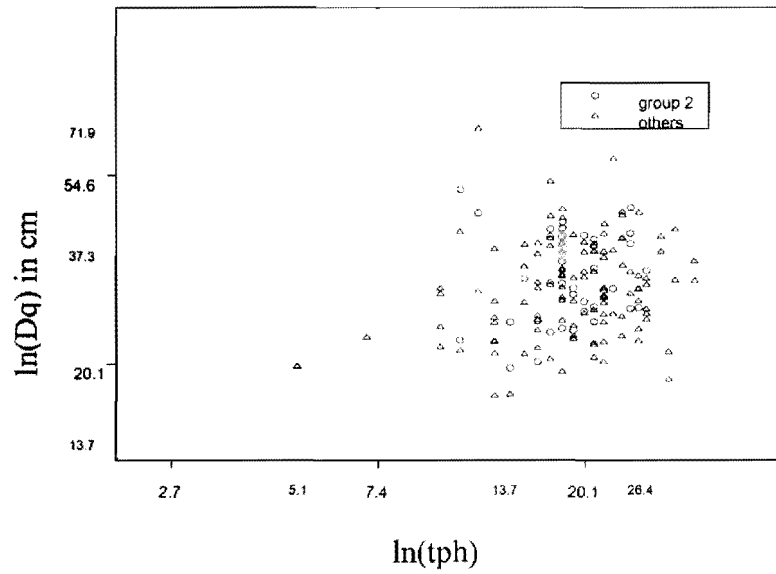


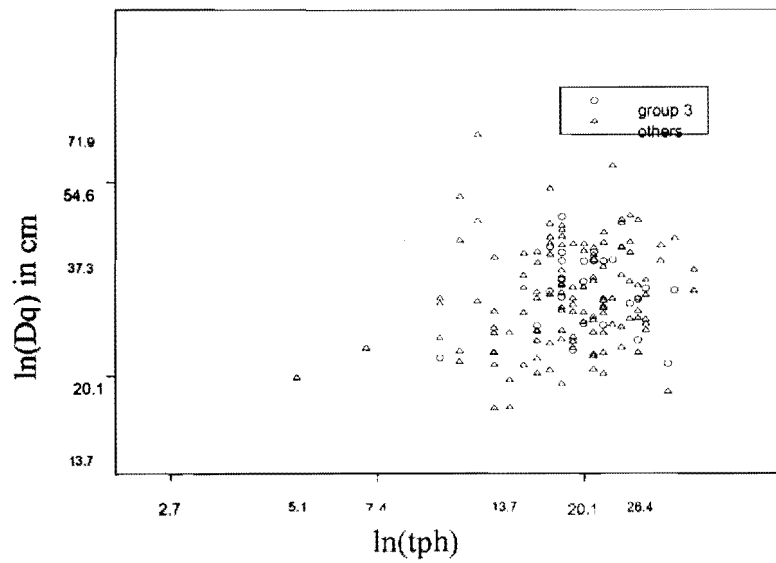
Figure 5: Scatter plot of the quadratic mean dbh (Dq) and trees per hectare (tph) for all Semangkok plots assuming six community types. Symbols differentiate (a) type 1, (b) type 2, (c) type 3, (d) type 4, (e) type 5, and (f) type 6 from others.



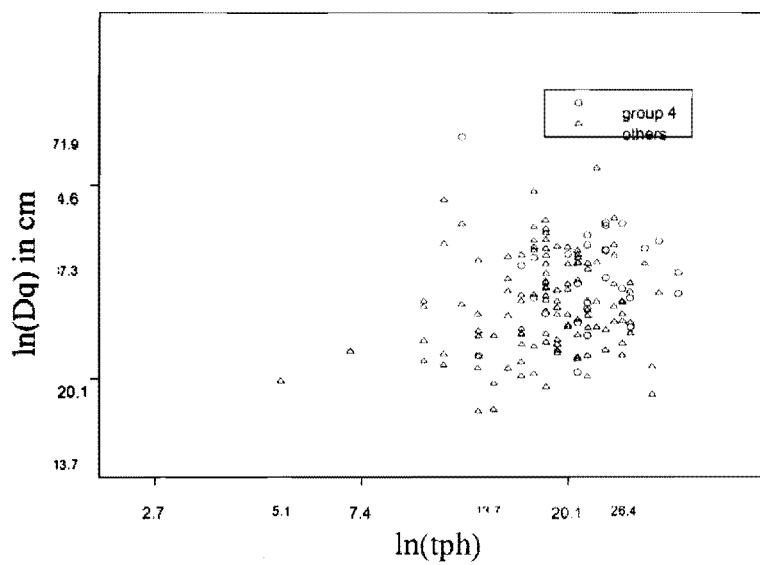
(b) Symbols differentiate type 2 from others



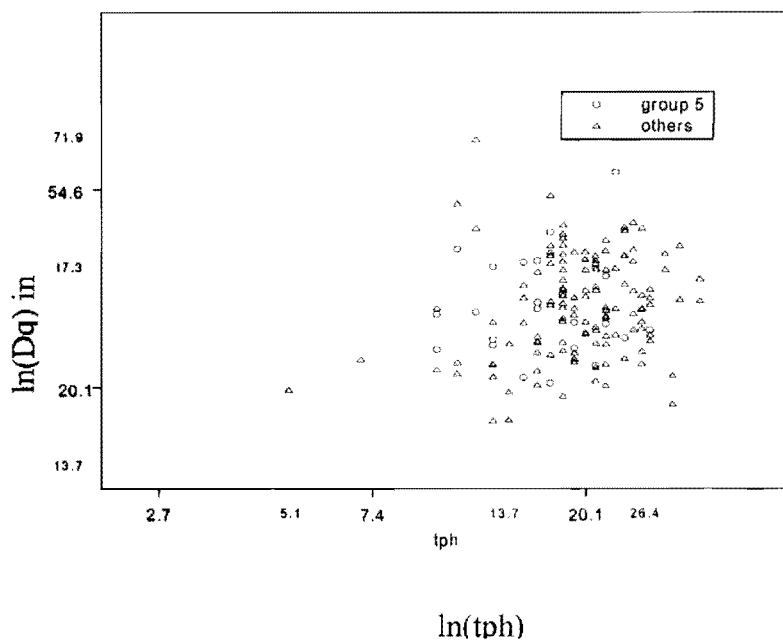
(c) Symbols differentiate type 3 from others.



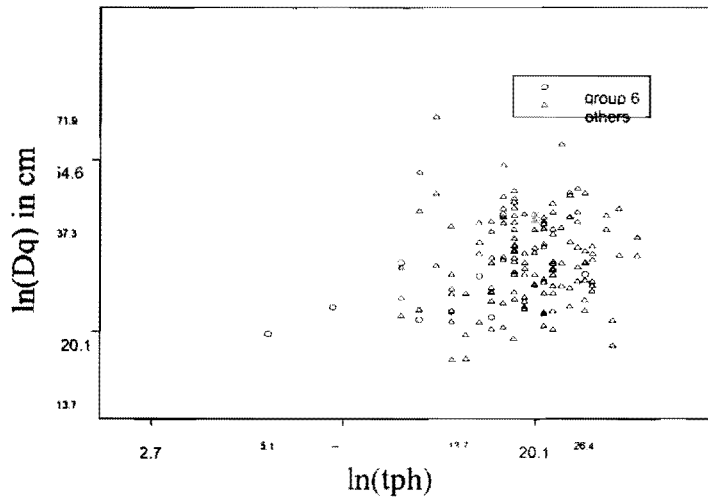
(d) Symbols differentiate type 4 from others.



(e) Symbols differentiate type 5 from others



(f) Symbols differentiate type 6 from others.



Gunung Ledang Inventory Nested Plots

Untransformed dbh distributions showed the best R^2 and lowest rmse for estimating the relationship between the $\ln(Dq)$ and $\ln(tph)$ in model [2]. All models with variance as the predictor showed better fits than models with skewness as a predictor. All models with skewness as a predictor have at least one insignificant variable. The model with variance of $dbh^{1.0}$ produced the best model, explaining 81 % of the variation in $\ln(Dq)$ (Table 13).

The all-subsets analysis allowing any combinations of skewness and variance of dbh^m yielded improved values of R^2 and FI with an increasing number of predictor variables, but there is an abrupt drop in FI with addition of a third predictor and another final drop with addition of a fifth variable. A parsimonious model requires it to be simple as possible while retaining relationships important for explaining silvicultural or biological mechanisms of the system; hence, the model below was selected as the most appropriate model to represent the maximum

size-density limit for Gunung Ledang. The model consisted of four predictors, which explained 83 % of the variation in $\ln(Dq)$ (Table 14). The model fit was significantly improved ($R^2 = 0.83$) by incorporation of the variance and skewness of the dbh distribution into the equation:

$$\ln(Dq) = 4.06 + 0.000815 s^2 + (-0.0059 sk - 0.136)\ln(tph) \quad [6]$$

When the structural parameters were excluded, the model explained only 38 % of the variation. The slope term was negatively related to skewness (Figure 6) while the intercept of equation [6] was positively correlated with the variance of the dbh distribution (Figure 7). The effect of variance on the intercept was more obvious than the effect of skewness on the slope (Figure 8).

Table 13: Results of regression analysis with $\ln(Dq)$ as dependent variables and $\ln(tph)$ with stand skewness and variance in model [2] for Gunung Ledang nested inventory plots (N=529)

Models	Variables	rmse	R^2
	$\ln(Dq) = a_0 + a_1 \ln(tph)$	0.38	0.15
1	$sk(dbh^1)^{n.s.}, sk(dbh^1):tph^{n.s.}, tph$	0.39	0.15
2	$sk(dbh^{1.5})^{n.s.}, sk(dbh^{1.5}):tph^{n.s.}, tph$	0.40	0.15
3	$sk(dbh^2)^{n.s.}, sk(dbh^2):tph^{n.s.}, tph$	0.40	0.15
4	$sk(dbh^{2.5})^{n.s.}, sk(dbh^{2.5}):tph^{n.s.}, tph$	0.40	0.15
5	$s^2(dbh^1)^{n.s.}, s^2(dbh^1):tph, tph$	0.81	0.09
6	$s^2(dbh^{1.5})^{n.s.}, s^2(dbh^{1.5}):tph, tph$	0.75	0.10
7	$s^2(dbh^2)^{n.s.}, s^2(dbh^2):tph^{n.s.}, tph$	0.66	0.11
8	$s^2(dbh^{2.5})^{n.s.}, s^2(dbh^{2.5}):tph^{n.s.}, tph$	0.59	0.13

rmse is residual mean square error, n.s. : not significant

tph is $\ln(tph)$

Extra-sum of square tests on community type indicator variables indicated significant predictive power under classifications with two, three or four community types (Table 15). However, only the community typing with two types gave consistently significant effects of each community type. An indicator variable for community type two in the two-cluster model was incorporated into the selected

model of structural parameters to determine if the combination improved the prediction of $\ln(Dq)$. Results indicated the combination of the structural parameters and community type produced a only slightly better fit than models with just structural parameters as predictors.

Table 14: Results of all-subset regression analysis of model [3] using structural parameters (skewness and variance) of dbh raised to varying powers as predictors for Gunung Ledang nested inventory plots

Variables	Cp	p	R ²	rmse	FI
s ² (tph)	3090.2	2	51.0	0.138	4.25
s ² a(tph)	3424.2	2	46.5	0.144	4.43
(tph),s ²	944.4	3	80.8	0.088	2.72
s ² ,sk(tph)	1311.8	3	80.3	0.098	3.04
(tph),sk,s ²	815.5	4	82.8	0.084	2.59
(tph),s ² ,sk(tph)	828.2	4	82.6	0.084	2.6
(tph),sk,s ^{2ns} ,s ² (tph)	755.5	5	85.0	0.082	2.53
(tph),sk,s ² ,ska(tph)	761.4	5	84.8	0.082	2.54
(tph),sk,s ^{2ns} ,s ² (tph),ska(tph)	694.8	6	86.6	0.080	2.47
(tph),sk,s ^{2ns} ,s ² (tph),skb(tph)	710.4	6	86.4	0.080	2.49
(tph),sk,ska,s ² ,s ² a,s ² b	634.4	7	89.2	0.078	2.41
(tph),sk,s ^{2ns} ,s ² c,s ² (tph),ska(tph)	649.2	7	88.6	0.078	2.42
(tph),sk,s ² ,s ² a,s ² c,s ² (tph),ska(tph)	523.5	8	90.7	0.074	2.29
(tph),sk,s ² ,s ² c,s ² (tph) ^{ns} ,s ² a(tph),ska(tph)	528.8	8	90.3	0.074	2.3
(tph),sk,s ² ,s ² a,s ² b,s ² c,s ² (tph),ska(tph)	138.9	9	91.8	0.058	1.8
(tph),sk,ska,skb,s ² ,s ² a,s ² b,s ² (tph)	410.1	9	91.7	0.070	2.16
(tph),sk,ska,skb,s ² ,s ² a,s ² b,s ² c,s ² (tph)	47.5	10	92.7	0.054	1.67
(tph),sk,ska,s ² ,s ² a,s ² b,s ² c,s ² (tph),ska(tph) ^{ns}	109.8	10	92.5	0.057	1.76

n.s. : not significant at 5% probability level

p is the number of co-variates in the model

tph is $\ln(tph)$

Explanation for sk,ska,skb,skc, s²,s²a,s²b and s²c is given in Table 3.

Figure 6: The relationship of slope to changes in skewness of dbh distribution of Gunung Ledang plot data

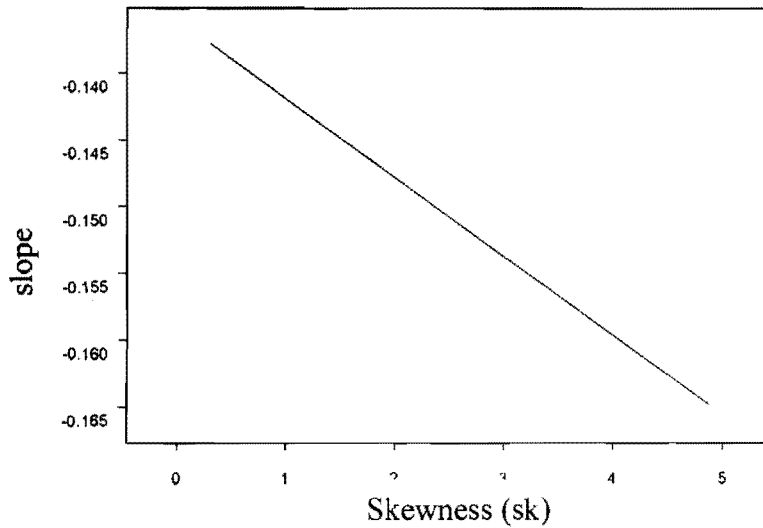


Figure 7: The relationship of intercept of equation [6] to changes in variance of dbh distribution of Gunung Ledang plot data.

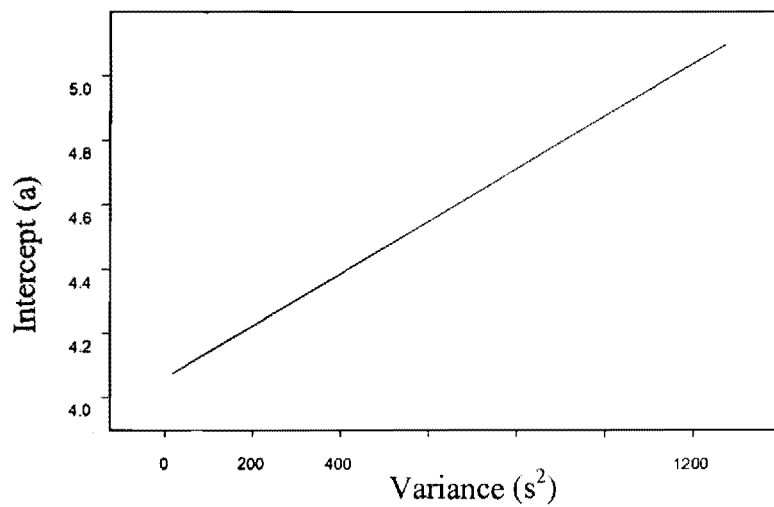


Figure 8: The maximum size-density line for model [6] under four conditions; a) $\max s^2$, $\max sk$; b) $\max s^2$, $\min sk$; c) $\min s^2$, $\max sk$; and d) $\min s^2$, $\max sk$

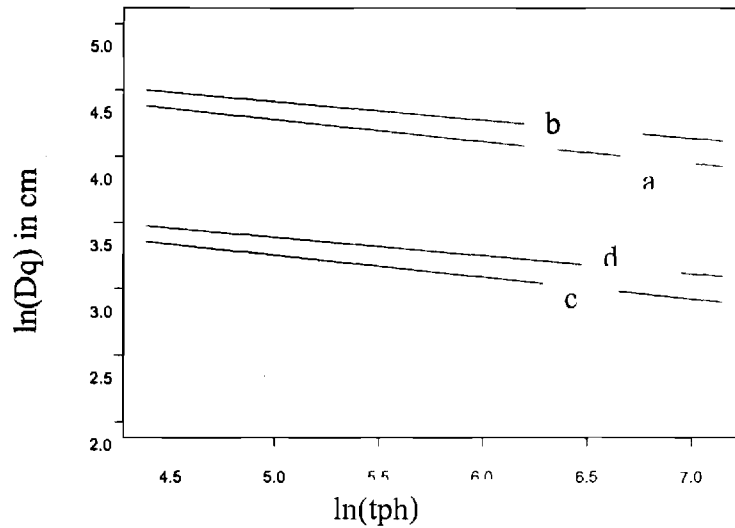


Table 15: Summary results of extra sums of squares tests on the effect of community type on the maximum size-density line equation [4] for Gunung Ledang nested inventory plots (N=529)

Number of clusters		coefficient k value				ESS F-test (P-value)
		0	1	2	3	
Two	d_k	4.760	-0.338			0.0001
	e_k	-0.225	0.053			
Three	d_k	4.736	-0.368	-0.054 ^{ns}		0.0003
	e_k	-0.221	0.058	-0.008 ^{ns}		
Four	d_k	4.762	-0.442	-0.030	0.075 ^{ns}	0.0003
	e_k	-0.224	0.071	0.004	-0.012 ^{ns}	

“^{ns}” indicates non-significant predictor with $\ln(Dq)$ at $P\text{-value} < 0.05$. ESS is the extra sum of squares for the F-test.

Evidence of Consistent Maximum Size-Density Trajectory from Repeated Measures Plot

The two long-term permanent sample plots follow trajectories strongly suggesting a maximum size-density limit. The stand trajectories deviated from the average self-thinning slope for short periods of mortality and recruitment, but returned to a size-density limit with consistent slope after a few years (Figure 9). The periodic changes in mortality and ingrowth and their mean diameter are illustrated in Figures 10-14. The deviation of the stands from, and subsequent return to an asymptote with common slope reflected resumption of self-thinning after recruitment and residual growth (Appendix 1a and 1b). Interpretation of the size-density stand trajectory differs by plot.

Case 1: Bukit Lagong plot

The first five measurements over a period of ten years showed mixed forest stand dynamics in which the size-density trajectory deviated temporarily from the maximum size-density line. In the first measurement period (1949-1951), the quadratic mean dbh and trees per hectare decreased due to mortality of upper canopy trees. In the second period (1951-1953), the number of trees increased due to ingrowth, but the quadratic mean dbh remained low or decreased both because ingrowth trees reduced mean diameter and because some large trees were still dying (Figure 11). In the next four years period (1953-1957), the quadratic mean dbh began to increase from 30.9 cm to 31.4 cm, but the increase in number of trees was minimal. The following years from 1959 to 1975 showed a steady increase in the quadratic mean dbh and decrease in number of trees per hectare within a slope of -3.42. There was a slight decrease in the quadratic mean dbh from 1971 to 1975, but an increase in the following period. Similar patterns with a generally consistent slope of the maximum size-density line were observed from 1985 to 1997. Analysis

of concurrent changes in D_q , ingrowth and mortality confirm these patterns (Figures 11-12).

Case 2: Sungei Menyala plot

The size-density trajectory followed a stable maximum size-density limit from the first measurement in 1947 to 1961 (Figure 9). The number of trees decreased while the mean dbh increased with self-thinning and survivor growth. During the period, ingrowth and mortality still occurred with slightly greater mortality than ingrowth (Appendix 1b). An abrupt change in the trajectory began in 1963. The number of trees dropped from 486 in 1961 to 462 trees in 1979, but subsequently increased to 484 trees in 1981. The number of trees decreased during the 1961-1963 growth period, but the quadratic mean dbh remained almost the same, indicating two possibilities; 1) the mean dbh of mortality was approximately equal to the mean dbh of trees initially present, and 2) mortality occurred in smaller trees than average. Between 1975 and 1977, the number of trees and quadratic mean dbh decrease remarkably, indicating relatively rapid mortality of larger trees and slower ingrowth of smaller trees. Little change occurs in number of trees between 1977 to 1979, the number of trees increased rapidly between 1979 and 1981; however, the quadratic mean dbh remained almost constant.

Figure 9: Maximum size-density trajectory for primary dipterocarp density based on long-term measurements for Bukit Lagong and Sungei Menyalaplots over successive occasion of measurements

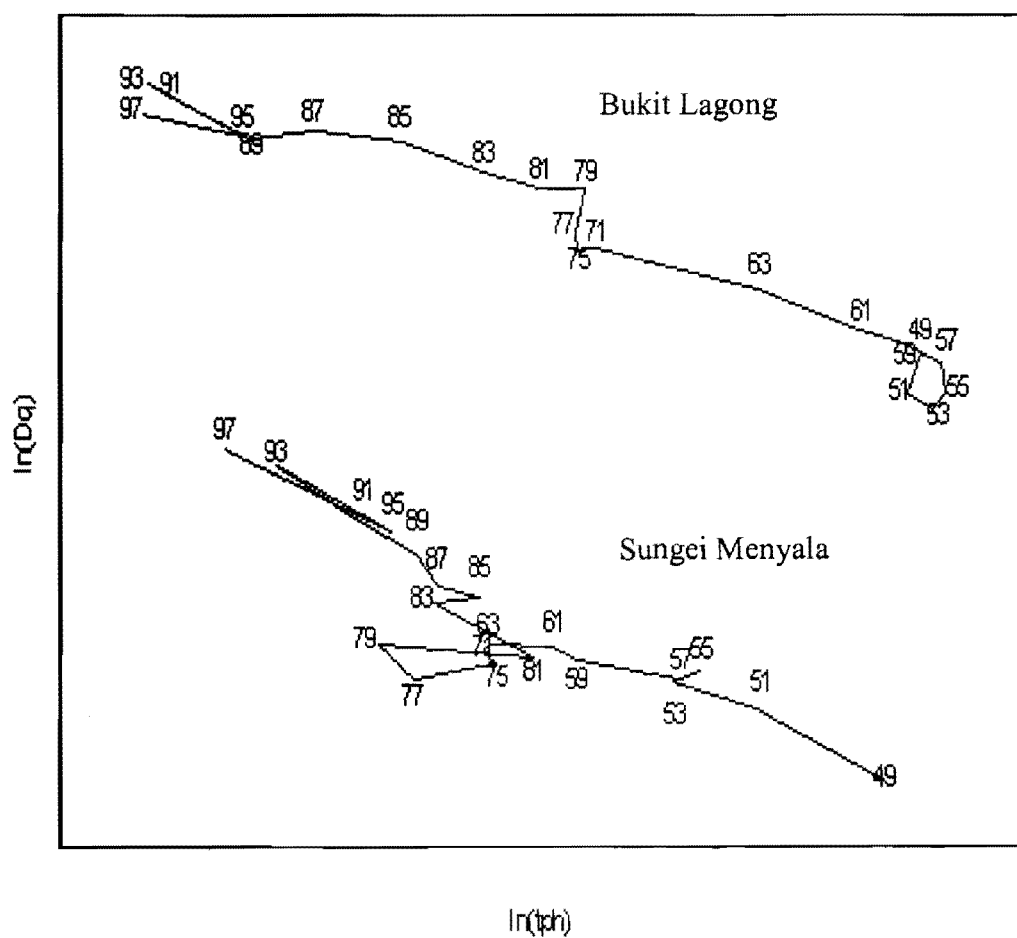


Figure 10: Quadratic mean dbh(Dq) and stocking of trees per hectare (tph) over successive years of measurements

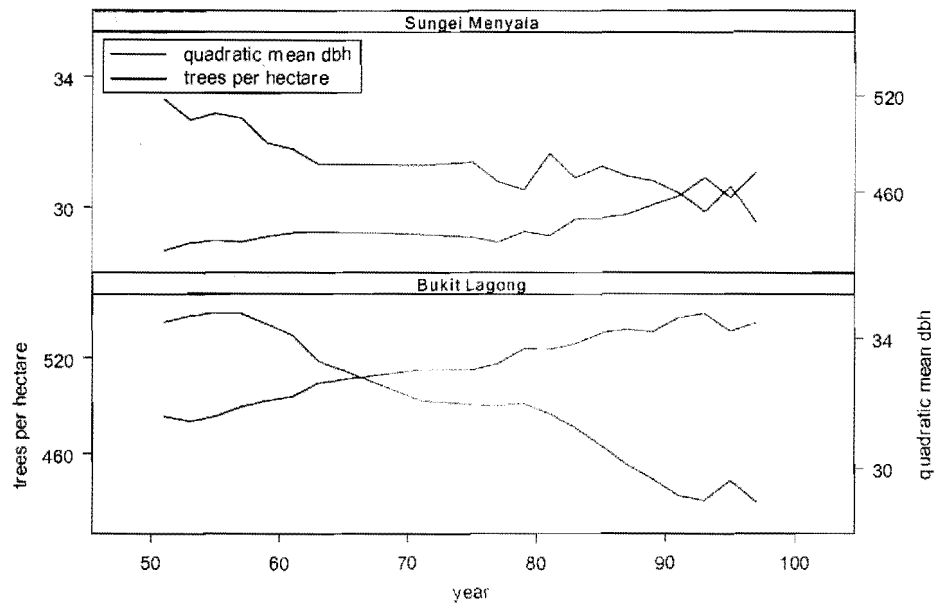


Figure 11: Quadratic mean dbh (Dq) and trees per hectare of periodic mortality over successive years of measurements

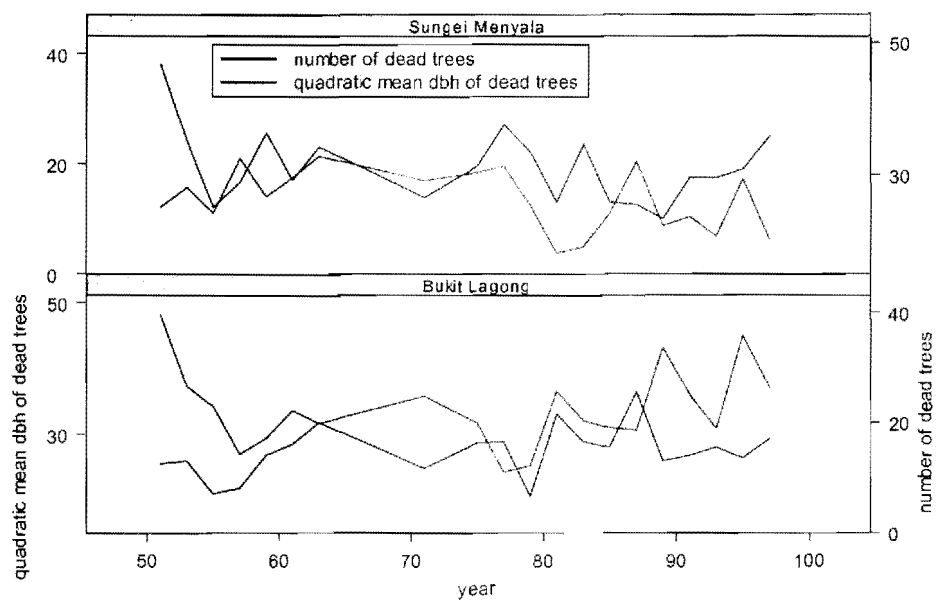


Figure 12: Quadratic mean dbh (Dq) and trees per hectare of periodic growth over successive year of measurements

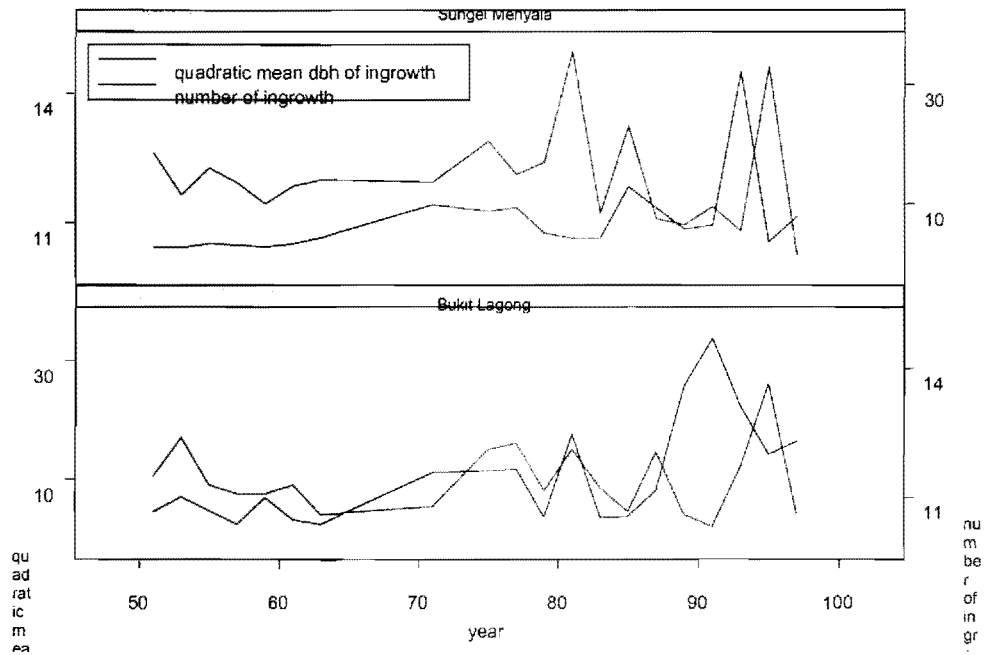


Figure 13: Skewness and variance of dbh distributions over successive years of measurements

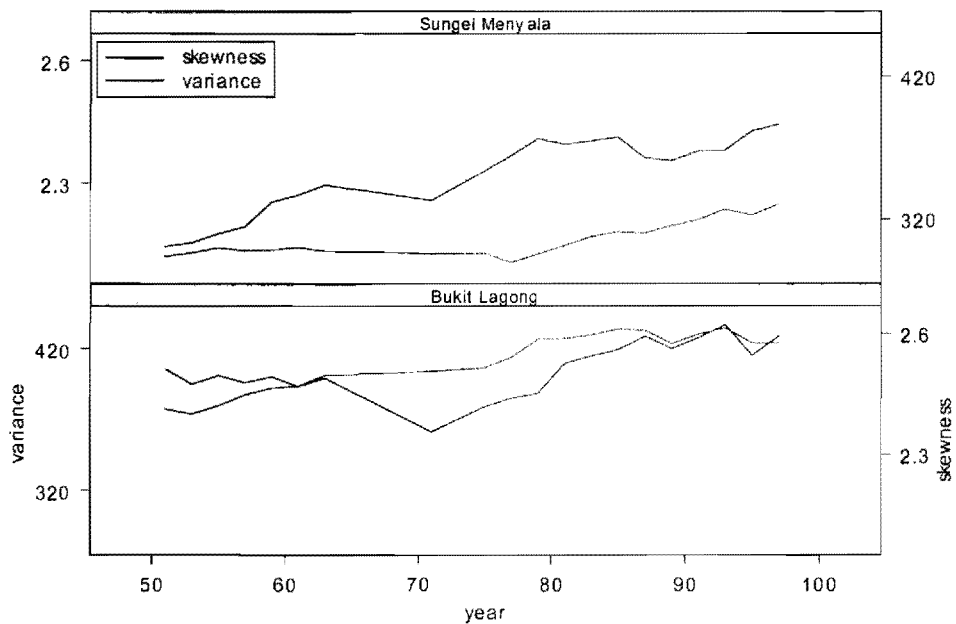
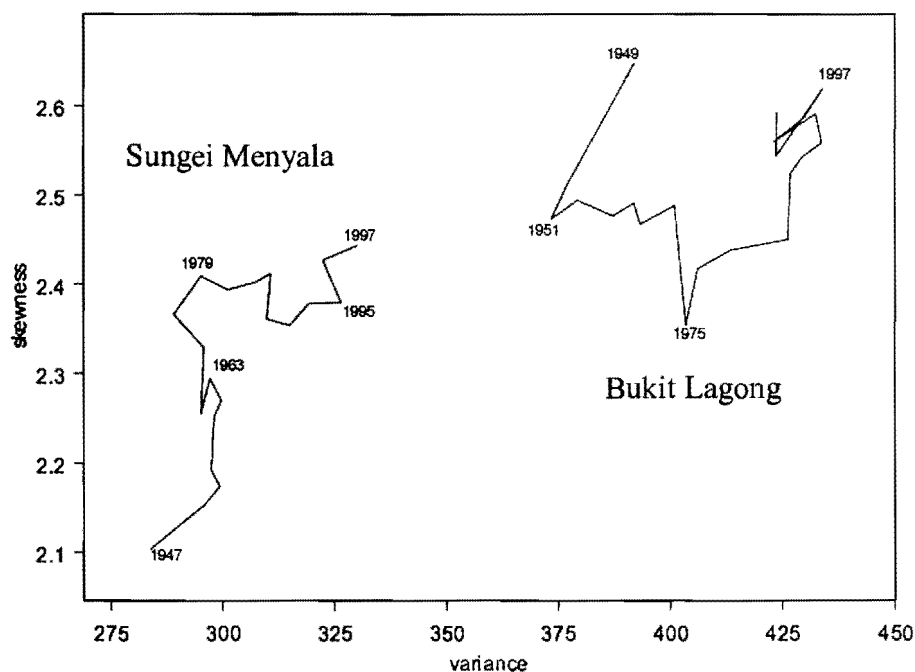


Figure 14: Scatter line plot of skewness and variance of dbh distribution for Bukit Lagong and Sungei Menyala plots over successive years of measurements



Maximum Density Line Based on Repeated Measure Plot

The regression line of $\ln(Dq)$ on $\ln(tph)$ indicated a maximum size-density slope of (2.54) (SE= 0.14). The results indicated a significantly different parameter estimates of $\ln(Dq)$ as compared to the hypothesized estimates of 1.6 (Reineke 1933) and 2.0 Manokaran and Swaine (1995).

$$\begin{aligned} \text{Ordinary least square slope of } \log(Dq) \text{ on } \log(tph) &= (\Sigma xy / \Sigma y^2) \\ &= -2.54 \end{aligned}$$

$$\begin{aligned} \text{Ordinary least square slope of } \log(tph) \text{ on } \log(Dq) &= (\Sigma xy / \Sigma x^2) \\ &= -0.37 \end{aligned}$$

The reciprocal of slope of $\log(Dq)$ on $\log(tph)$, however is -2.68, slightly higher than -2.54. The GMR slope of $\log(Dq)$ on $\log(tph)$ gave slightly higher value than the ordinary least square.

$$\begin{aligned}\text{GMR slope of } \log(Dq) \text{ on } \log(tph) &= s_y/s_x \\ &= (y^2/x^2)^{0.5} \\ &= (0.022951/0.15673)^{0.5} \\ &= 2.61\end{aligned}$$

$$\text{GMR slope of } \log(tph) \text{ on } \log(Dq) = 0.38$$

Using the GMR method, the reciprocal of slope of $\log(Dq)$ on $\log(tph)$, is symmetrical i.e. equivalent to 0.38.

Trends in Long Term SDI Trajectory over Successive Years of Measurements based On Equation from Gunung Ledang Inventory Plots

The long-term trajectory of sdi to the Bukit Lagong and Sungei Menyala plot using structural parameters identified in fitting model [3] for Gunung Ledang (see equation [6]):

$$sdi = \exp(-b_0/b_1)/25.4^{-1/b}$$

$$b_0 = 4.06 + 0.000815 \cdot s_2$$

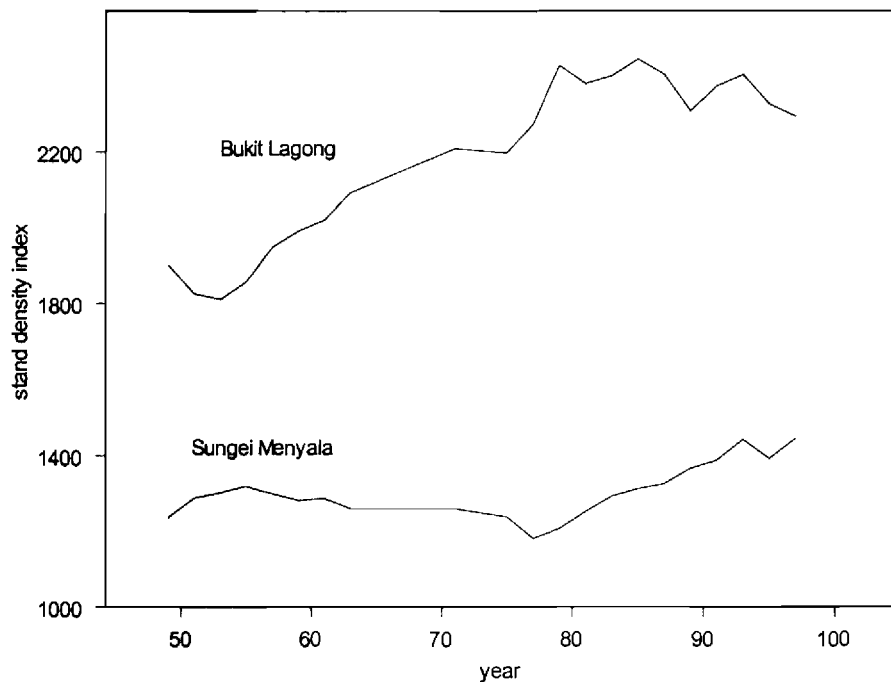
$$b_1 = -0.136 - 0.0059 \cdot s_k$$

Bukit Lagong plot showed an overall increasing trend. However, the increase in sdi occurred at a short period at three occasions, between year 1951 to 1957, 1975 to 1979, and 1993 to 1995. In 1953 to 1955 the decrease and increase in sdi reflects changes in growth components, i.e., tree growth vs. mortality vs. ingrowth of trees into the lowest size class. The vertical increase in the mean size (Figure 9) from 1953 to 1957 was reflected in the increase of sdi during the period.

Similar changes were also shown from 1975 to 1979. The increase of sdi from 1993 to 1995 is due to the increasing number of trees from ingrowth, although there is a slight decrease in mean size (Figure 15).

Sungei Menyala plot showed a more stable sdi over the successive measurement as compared to Bukit Lagong plot. In the initial stage, the plot showed a generally decreasing trend, but later more or less stabilized and fluctuated at a more stable sdi between 1963 and 1997. All trajectories showed a decline in the sdi from 1975 to 1977, but later increased to their previous level in 1981 (Figure 15).

Figure 15: Long-term sdi trajectory of Bukit Lagong and Sungei Menyala plot based on the equation [6]



Effects of Spatial Scale on the Distribution of the Maximum Size-Density Limit

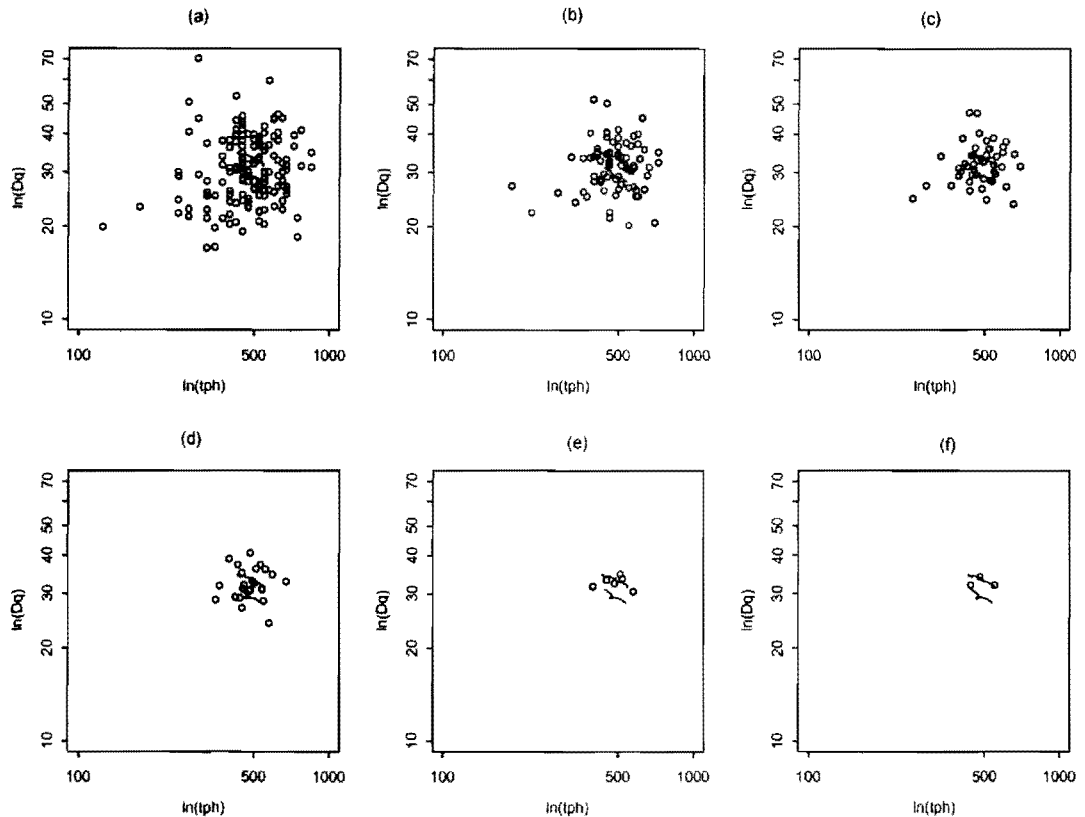
A wider variation in the $\ln(Dq) \sim \ln(tph)$ relationship was observed for smaller spatial scales (Figure 16). Some plots had unrealistically high $\ln(Dq) \sim \ln(tph)$ combinations, while others did not exhibit full carrying capacity. The larger spatial scale provided a more stable $\ln(Dq) \sim \ln(tph)$ maximum, closer to the maximum size-density trajectory of Bukit Lagong. An appropriately large scale is necessary to examine maximum size-density limits for uneven-aged, mixed-species forests.

DISCUSSION

Inferences from Temporary Plots

Regression analysis indicated that the size-density relationship was affected by stand structural parameters, but weakly correlated with species composition of the stand. Stand structure was significantly related to the Dq - tph relationship through the variance and skewness of the diameter distribution on temporary plots at Semangkok and Gunung Ledang. However, the specific structural parameters that influenced the size-density limit differed between the sites. In the Semangkok plot, the regression intercept was influenced by the natural logarithm of the variance of $dbh^{1.5}$, and slope by the variance of dbh . In Gunung Ledang, the intercept was a function of the variance and slope was a function of the skewness of the dbh distribution. The plots in Semangkok were contiguous 20 x 20 m plots, while Gunung Ledang were scattered across a grid and sampled over a larger area.

Figure 16: Size-density distribution of trees in Semangkok 6-ha plot at six spatial scales (a) 0.04 ha (b) 0.08 ha (c) 0.12 ha (d) 0.24 ha (e) 1.00 ha (f) 2.00 ha. The size-density trajectory of Bukit Lagong and Sungei Menyala plot were also shown



The Gunung Ledang size-density relationship is more representative of the size-density relationship of typical hill dipterocarp forest than Semangkok plot, as it covers a wider area and large number of plots. On both plots the size-density model explained more than 80% of the variation in D_q when structural parameters were included. However, it was not appropriate to conclude that this relationship was the maximum density limit of hill dipterocarp forest. The equation could be used to predict expected D_q for a given stand structure.

Sterba and Monserud (1993) stated that the more skewed the $DBH^{1.5}$ distribution of a stand, the less steep the maximum density line where $\ln(tph)$ is plotted on $\ln(D_q)$. Very uneven-aged stands with large skewness and reverse J-

shaped diameter distributions have nearly vertical maximum density line when $\ln(Dq)$ is plotted on $\ln(tph)$. This means that these stands may have nearly any quadratic mean diameter without having very different maximum stem numbers as long as their structure (skewness) is the same. Sterba and Monserud (1993) had demonstrated that the maximum size-density limit is influenced by structural parameters and habitat types in mixed conifer forest of western North America. Our analysis also indicated that, at fine spatial scales, a close relationship exists between stand structural parameters and the size-density relationship for both Gunung Ledang nested plot and Semangkok contiguous plot.

Biological Interpretation of the Interplay between Apparent Stand Density, Autogenic Disturbances and Stand Structure.

The model developed from temporary plots in Semangkok and Gunung Ledang did not reflect a maximum growing capacity of a fully stock stand. The slope of the maximum size-density line (equation 1) for Semangkok ranges between 0.0054 – 0.0536, and that for Gunung Ledang ranges between 0.107 – 0.134. The value is much lower than the hypothesized value of 0.605 based on Reineke (1933) or 0.5 based on maximum basal area (Manokaran and Swaine 1995) when $\ln(Dq)$ is regressed on $\ln(tph)$. In the Semangkok plot, the $\ln(Dq)$ - $\ln(tph)$ relationship was highly variable between plots at the 20m scale, and could be attributed to differences in successional status after disturbance such as wind-throw, landslide, lightning strike, or dominance of other vegetation not accounted for in the analysis. At Semangkok, 15.6 percent of the stand is represented by canopy gaps below 10 m height (Niiyama et al. 1999). On the ridge and upper slope of the Semangkok plot, undergrowth was dominated by *Eugeissona triste* stemless palms. Abundance of *Eugeissona triste* affects stand structure by precluding smaller-size trees. Large trees are generally confined to stable ground, e.g., on the ridges and more gentle valley. On steep slopes the soils are shallower

and less stable for large trees, which make them prone to wind-throw. The differences in community structure, however was not associated with stand structure.

Despite a high variability among plots the model produced a high R^2 value implying a good prediction of $\ln(\text{tph})$ under a given set of $\ln(\text{Dq})$ and structural parameters. The intercept and slope value of the equation can be used to calculate the stand density index using equation 6. Using this approach, the calculation of sdi is not fixed at a certain maximum size-density slope, but varies by stand structure.

Interpretation Based on Previous Work by Manokaran and Swaine

Some evidence has been suggested for a constant maximum basal area based on long-term ecological plots in primary dipterocarp forest (Manokaran and Swaine 1994) and on comparisons of primary and regenerated (Manokaran 1998) lowland dipterocarp forest. If the maximum size-density limit is a fixed basal area, the slope on the $\ln(\text{Dq}) \sim \ln(\text{tph})$ line is implied to be -2 . Our analysis using long-term measurements of the Bukit Lagong plot revealed that the maximum size-density slope was steeper at -2.62 , implying a non-constant maximum basal area. With lines of differing slope intersecting at $\text{Dq}=25.4$, the steeper maximum size-density slope implies a lower number of trees per hectare for stands with $\text{Dq}>25.4$ cm, suggesting that the trees occupy more growing space per unit area.

Inferences from Permanent Plots

Although both plots showed similar patterns of maximum size-density trajectories in relation to changes in overall stand dynamics, there are fundamental differences in terms of Dq and the variance of dbh. The Dq and variance of dbh in Bukit Lagong were markedly higher than in Sungei Menyala plot (Figure 14;

Appendix 2). The maximum stand basal area of Sungei Menyala (33.6 m²/ha) is approximately 75% of Bukit Lagong (43.8 m²/ha). Manokaran and Swaine (1994) found that the total basal area of all 10-cm dbh classes was higher in Bukit Lagong than in Sungei Menyala, except for size class 10 cm and 80 cm. The higher variance in Bukit Lagong implies a wider variety of size classes.

The topography and soil condition between the sites differ. Sungei Menyala is situated 30 m above sea level. The land is fairly flat. At the study site itself soil is mainly moderately well-drained to poorer-drained alluvium derived from granite (Wyatt-Smith 1987). Bukit Lagong is situated at an altitude of 460-550m above sea level, with a range of 80m within the sample plot encompassing the ridge-top, steep side-slope and small valley bottom of a hill covering 28 %, 52% and 20 % of the plot, respectively.

The Sungei Menyala (sungei=river) plot has been identified as Red Meranti-Keruing forest of the West Coast type Wyatt-Smith (1987) and belongs to the lowland dipterocarp forest. In contrast, Bukit Lagong (bukit=hill) belongs to the hill dipterocarp forest of Seraya-Ridge and Balau Kumus sub-type (Wyatt-Smith 1963). Both forest are classified as dipterocarp due to the predominance of the Dipterocarpaceae family. These forests can be classified as having three major layers, the emergent layer, main canopy layer and the intermediate or understorey layers. The fundamental difference in the vegetation is the species composition. According to Manokaran and Swaine (1994) the emergent layer at Sungei Menyala forest reserve is dominated by *Shorea parvifolia*, *S. macroptera*, *S. pauciflora*, *S. leprosula*, *S. ovalis*, *S. hopeifolia*, *S. acuminata*, *Dipterocarpus verrucosus* and *D. crinitus*. Common emergents from other families are *Dyera costulata* (Apocynaceae), *Koompassia malaccensis* (Leguminosae), *Heriteria simplicifolia* (Sterculiaceae), *Palaquium rostratum* (Sapotaceae) and *Dialium platysepalum* (Leguminosae). The most abundant species are *Shorea curtisii* (Seraya) and *S. laevis* (balau kumus). Other Dipterocarpaceae which are represented in the emergent layer are *Neobalanocarpus hemii*, *Anisoptera curtisii* and *Dipterocarpus*

costatus. Common emergents from other families are *Koompassia malaccensis* (Leguminosae) and *Myristica maingayi* (Myristicaceae).

The differences in topography, site and vegetation factors might contribute to the maximum carrying capacity of the stand. Investigation of the maximum size-density limit in other ecological plots of similar condition and plot size may reveal further insight on the maximum carrying capacity of primary dipterocarp forest.

Recommended Position of Size-Density Limit for Hill Dipterocarp Forest

Two types of regression analysis have been tested to determine the maximum size-density slope for hill dipterocarp forest, namely ordinary least square method, and geometric mean regression. The test on the slope of the maximum size-density limit was based on equation 1 and indicated that the slope was higher than both Reineke's slope and the slope implied by a maximum basal area. A key question that arises for applying the maximum size-density limit to hill dipterocarp forest is the appropriate slope and intercept of the maximum line. The slope differed when the regressor and predictor switch interchangeably under ordinary least squares. Using the geometric mean regression method, the maximum density line remained symmetrical, in the sense that if $\ln(\text{tph})$ and $\ln(\text{Dq})$ were interchanged, the computed slope was replaced by its reciprocal. In this respect, the recommended slope for a working model in the hill dipterocarp forest should follow the geometric mean regression approach (Ricker 1984). This avoids the controversy as to whether $\ln(\text{Dq})$ should be regressed on $\ln(\text{tph})$ or $\ln(\text{tph})$ on $\ln(\text{Dq})$.

Influence of Spatial Scale on Size-Density Relationship

Results indicated that spatial scale affects the distribution of the $\ln(Dq) \sim \ln(tph)$ relationship. A finer spatial scale produces $\ln(Dq) \sim \ln(tph)$ relationships that are unrealistically high or low relative to the actual maximum growing capacity of the stand.

The differences in the nature of the $\ln(Dq) \sim \ln(tph)$ relationship can be related to the growth cycle, size structure and community structure of the stand. The death of an individual tree or group of trees create a gap in the forest canopy into which other trees grow, mature and eventually die again (Whitmore 1984). The forest canopy is continually changing as mortality, recruitment and growth of surviving trees occurs. In the Semangkok plot, 15.6 percent of the stand is represented by canopy heights below 10 m (Niiyama et al. 1999).

Selection of plot size in forest research is influenced by intended purpose, by stand conditions, by expected duration of study, and by cost considerations (Curtis 1983). For example, Synott (1980) suggested that silvicultural plots must be large enough to intergrate both local variability of the forest (such as single tree gaps, etc) and the impact of treatments in tropical rain forests.

Variability generally decreases with increasing plot size, and plots that are excessively small relative to the pattern of within-stand variation will produce considerable range of values for variables such as density and volume (Smith 1975). In relatively uniform, even-aged stands of a single species, or in plantations plot sizes typically range from 0.1 to 0.2 ha. Uneven-aged mixed species stands are inherently variable and require larger plots to characterize the stand structure and growth (Curtis 1983). Mixed tropical forests are notably heterogenous at a local scale, so variances increase as plot size decreases (Alder and Synott 1992). Vancley (1994) stated that plot size should be sufficiently small that the plot is homogenous, at least with respect to forest type and site productivity, and sufficiently large to

provide a representative sample of the forest stand. In tropical mixed forest, a plot size of 1-ha has been recommended for growth studies (Synott 1979; Alder and Synott 1992).

Using a smaller plot size is subject to the possibility that a plot falls on extreme stand condition due to outside disturbances, for example, a local landslide on a hill slope, or tree-fall gaps caused by the death of very large over-mature trees. In one incidence a group of standing trees on the ridge and upper slope were dying, probably due to a lightning strike. Although, community structure has no significance influence on the maximum density limit, the dbh distribution on 20 x 20 m plots could be affected by its topographic position. The ridges generally had more large trees due to the predominance of Seraya and dominance of bertam palms (*Euzeissona triste*) below the main canopy. Steeper slopes makes the soil less stable for supporting large trees. The influence of topographic position on maximum density needs further investigation. Our results on the influence of spatial scale on the variability of $\ln(Dq) \sim \ln(tph)$ relationship indicated a larger plot of 1-2 ha provided a more realistic and stable maximum size-density limit for primary hill dipterocarp forest.

CONCLUSIONS

The evaluation of maximum size-density limits and their dependence on stand structure in primary hill dipterocarp forest showed several interesting insights based on a large sample of temporary plots:

- a) The best predictive power for the slope and intercept of the size-density limit was obtained from $dbh^{1.0}$; that is, the lowest rmse and the highest R^2 values were obtained under no transformation of dbh,





- b) The mean size (D_q) can be well predicted given the stand density and structural parameters of the size distribution, but does not have any significant relationship to species composition as represented by community types,
- c) Spatial scale affects maximum density limit of uneven-aged and mixed-species stands of primary hill dipterocarp forest. A plot covering 1-2 ha is essential for assessing the maximum size-density limit in this forest type.

Several conclusions can be drawn from the long-term size-density trajectories of permanent plots in primary dipterocarp forest:

- a) There is evidence of a consistent and stable maximum size-density limit for primary lowland and hill dipterocarp forest,
- b) Temporary deviation of stand trajectories from their asymptotic approach to a maximum size-density limit reflects tree recruitment and residual growth following individual tree mortality,
- c) The stand trajectories observed are consistent with gap phase dynamics observed in many forest types. As described by Zeide (1987), the degree of crown closure is simultaneously influenced by lateral crown growth and formation of new gaps by mortality.
- d) The general direction of the size-density trajectories indicated a decrease in tree number and increase in mean size over the period of measurement, as would be observed during self-thinning in an even-aged stand.

- e) The size-density trajectory can be divided into four categories: 1) negative decreasing, 2) negative increasing, 3) positive decreasing, and 4) positive decreasing trajectory. These categories are closely related to the number of trees that died or grew into the minimum specified dbh. Table 16 describes the component of stand dynamics that influence the trajectory.

Table 16: Size-density trajectory as influenced by ingrowth and mortality

Trajectory direction	<u>Mortality</u>		<u>Ingrowth</u>
	tph	Dq	tph
	high	large	low
	low	large	high
	high	small	low
	low	small	high

- f) The size-density trajectory moved in one of four possible directions besides vertically or horizontally, depending on the amount of mortality and ingrowth (Table 16). Size of the trees that die will have a strong effect on the trajectory, and indicate whether the trees died from suppression mortality vs. density-independent factors.
- g) The slope of the apparent size-density limit for both stands was more or less consistent. However, Bukit Lagong had a higher maximum size-density limit. This phenomenon prompts another interesting question; that is, can these behaviors be generalized to

other forest sites, or do lowland and hill dipterocarp forest have uniquely similar maximum size-density slope?

Although these findings provided an important initial assessment of maximum size-density limits for dipterocarp forests, to extrapolate the findings to other areas is not appropriate because similar long-term plots of this kind are not available. Another alternative would be to infer size-density limits from a large sample of temporary plots. Other factors that influence the maximum size-density line can also be examined. For example, Sterba and Monserud (1993) found that structural parameters and species mixture influenced the slope of the line, as was found at Gunung Ledang.

These results are important for effective management of uneven-aged, mixed species stands of dipterocarp forest. The status of a stand relative to its maximum size-density limit reflects the available growing space. Individual tree structure and, hence, stand structure is influenced by the relative density at which a stand is maintained. Likewise, relative growth rate among stands depends on their relative density. Concerns about growth stagnation in managed, fully-stocked, regenerated forests of Peninsular Malaysia have been raised by Wyatt-Smith (1963). He suggested that the basal area of regenerating forests approaching maturity should be kept below the basal area of a fully-stocked primary forest stand, thereby maintaining total stand increment and avoiding stagnation. It is generally regarded appropriate for residual levels of growing stock to be substantially below maximum carrying capacity after silvicultural treatment to promote growth of residual stand. Conversely, knowledge on the maximum carrying capacity for a particular stand is also required to project more reliably and realistically the site's potential and sustainable yield. Many if not most growth models for temperate species incorporate the maximum size-density concept to control mortality and keep stand density within rational limits (for example, Wykoff et al.(1986) and Hann and Wang 1990). Similarly, knowledge of the

maximum size-density limit has significant potential as a basis for evaluation of growth-growing stock relations in managed dipterocarp forests.

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APPENDICES

Appendix 1a:

Quadratic mean dbh (Dq), and trees per hectare (N) by year of measurement, and mortality and ingrowth of trees in the Bukit Lagong plot. Nm= trees per hectare dying in previous growth period, TBA=total basal area, Ni=trees per hectare growing into minimum size class over previous growth period, AMR=annual mortality rate, AIR=annual ingrowth rate.

Year	Dq (cm)	N (trees/ha)	Mortality				Ingrowth			
			Nm	AMR (%)	Dq	TBA	Ni	AIR (%)	Dq	TBA
1949	32.0	544.0	0.0	0.0	0.0	0.00	0.0	0.0	0.0	0.00
1951	31.6	542.0	12.5	1.2	48.1	2.27	10.5	1.0	10.7	0.09
1953	31.4	546.0	13.0	1.2	37.2	1.42	17.0	1.6	11.0	0.16
1955	31.6	548.0	7.0	0.6	34.2	0.64	9.0	0.8	10.7	0.08
1957	31.9	547.5	8.0	0.7	26.9	0.45	7.5	0.7	10.4	0.06
1959	32.1	541.0	14.0	1.3	29.4	0.95	7.5	0.7	11.0	0.07
1961	32.2	534.0	16.0	1.5	33.6	1.42	9.0	0.8	10.5	0.08
1963	32.6	518.0	20.0	1.9	31.6	1.57	4.0	0.4	10.4	0.03
1971	33.0	493.0	11.6	1.2	35.8	1.17	5.4	0.5	11.6	0.06
1975	33.0	490.5	16.3	1.7	31.7	1.28	15.0	1.5	11.6	0.16
1977	33.2	490.0	16.5	1.7	24.2	0.76	16.0	1.6	11.7	0.17
1979	33.7	491.5	6.5	0.7	25.2	0.32	8.0	0.8	10.5	0.07
1981	33.7	485.0	21.5	2.2	36.5	2.25	15.0	1.5	12.5	0.18
1983	33.8	476.5	16.5	1.7	32.1	1.33	8.5	0.9	10.5	0.07
1985	34.2	465.0	15.5	1.7	30.9	1.17	4.5	0.5	10.6	0.04
1987	34.3	453.0	25.5	2.8	30.5	1.87	14.5	1.6	11.2	0.14
1989	34.2	444.0	13.0	1.4	43.1	1.90	4.0	0.4	13.6	0.06
1991	34.6	433.5	14.0	1.6	36.0	1.42	2.0	0.2	14.7	0.03
1993	34.8	430.5	15.5	1.8	30.8	1.16	12.0	1.4	13.1	0.16
1995	34.2	443.0	13.5	1.6	44.9	2.14	26.0	3.0	12.0	0.29
1997	34.5	429.5	17.0	2.0	37.0	1.83	4.0	0.5	12.3	0.05

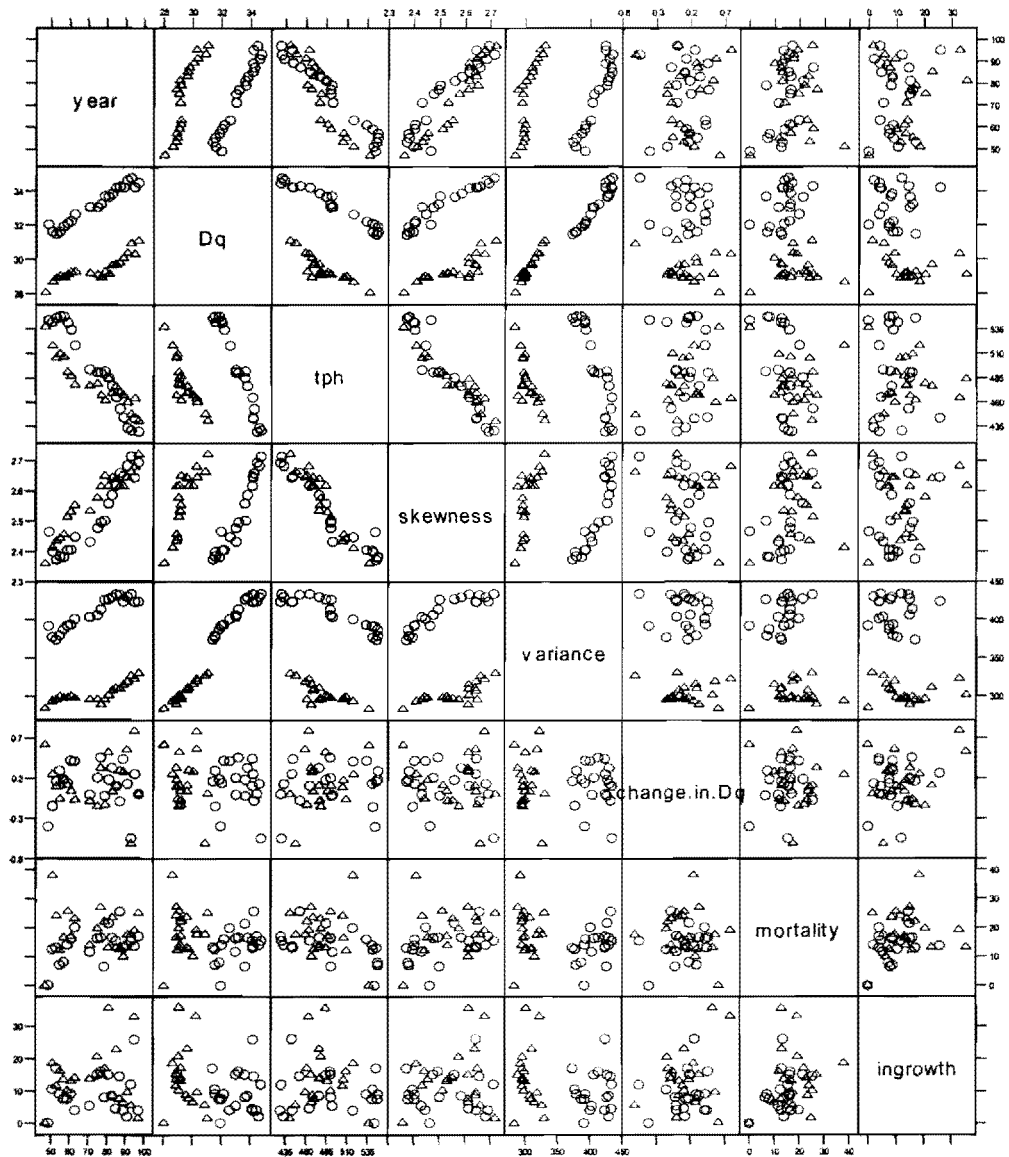
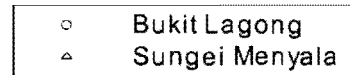
Appendix 1b:

Quadratic mean dbh (Dq), trees per hectare (N), mortality and ingrowth of trees in Sungei Menyala plot

Year	Dq (cm)	N (trees/ha)	Mortality				Ingrowth			
			N	AMR (%)	Dq	TBA	N	AIR (%)	Dq	TBA
1947	28.0	537.0	0.0	0.0	0.0	0.00	0.0	0.0	0.0	0.00
1951	28.6	517.5	38.0	3.7	25.1	1.89	18.5	1.7	10.4	0.16
1953	28.9	505.0	24.0	2.4	28.2	1.50	11.5	1.1	10.4	0.10
1955	29.0	509.0	12.0	1.2	24.2	0.55	16.0	1.6	10.5	0.14
1957	28.9	506.0	16.5	1.6	32.5	1.37	13.5	1.3	10.5	0.12
1959	29.1	490.5	25.5	2.6	26.7	1.43	10.0	1.0	10.4	0.09
1961	29.2	486.5	17.0	1.8	29.6	1.17	13.0	1.3	10.5	0.11
1963	29.2	477.5	23.0	2.4	32.8	1.95	14.0	1.4	10.6	0.12
1971	29.2	476.5	13.9	1.5	29.2	0.93	13.6	1.4	11.4	0.14
1975	29.1	478.5	19.5	2.1	30.4	1.42	20.5	2.2	11.3	0.20
1977	28.9	466.5	27.0	2.9	31.3	2.08	15.0	1.6	11.3	0.15
1979	29.2	461.5	22.0	2.4	25.4	1.11	17.0	1.8	10.7	0.15
1981	29.1	484.0	13.0	1.4	18.1	0.34	35.5	3.8	10.6	0.32
1983	29.6	469.0	23.5	2.5	19.1	0.67	8.5	0.9	10.6	0.08
1985	29.7	476.0	13.0	1.4	24.1	0.60	23.0	2.5	11.8	0.25
1987	29.8	470.0	12.5	1.3	32.1	1.01	7.5	0.8	11.3	0.08
1989	30.1	467.0	10.0	1.1	22.3	0.39	6.5	0.7	10.8	0.06
1991	30.3	459.5	17.5	1.9	23.7	0.77	9.5	1.0	10.9	0.09
1993	30.9	447.5	17.5	1.9	20.7	0.59	5.5	0.6	14.5	0.09
1995	30.3	463.5	19.0	2.2	29.4	1.29	33.0	3.7	10.5	0.29
1997	31.1	440.5	25.0	2.8	20.2	0.80	1.5	0.2	11.1	0.01

Appendix 2

Scatter plot matrix of key variables to explain the maximum size-density trajectory behavior of Bukit Lagong and Sungei Menyala plot over successive re-measurement



CHAPTER 3

EQUATIONS FOR PREDICTING ANNUAL DIAMETER INCREMENT FOR INDIVIDUAL TREES IN SECOND GROWTH HILL DIPTEROCARP FOREST

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EQUATIONS FOR PREDICTING ANNUAL DIAMETER INCREMENT FOR INDIVIDUAL TREES IN SECOND GROWTH HILL DIPTEROCARP FOREST

ABSTRACT

A nonlinear random species effects model for predicting diameter increment of trees in second growth hill dipterocarp forest was developed based on data from growth and yield plots at Tekam Forest Reserve. The plot was established after harvesting in 1978 and subsequently re-measured. Appropriate model form was examined and diameter increment model was selected to predict annual diameter increment. dbh, $\ln(\text{dbh})$, osdi, sdi and dmax were predictor variables selected from all-subset regression analysis. The inclusion of tree size parameters, influence the growth pattern that form a peaking behavior and asymptotic approaching to zero for larger size trees. Treating species as random effects on regression intercept and tree size coefficient reflects the biological growth properties of the species. Parameters were estimated using restricted maximum likelihood. Nested model were tested using likelihood ratio test. Two species classification were examined, ecological grouping and vernacular names. Comparisons between models were based on the AIC value (Atkaike Information Criterion). Treating species as random effects provide several advantages (a) the model form is common to all species, with slight perturbations to each parameter arising from the random species effect (b) all data are used in a single estimation algorithm. Although species were treated as random effects, the prediction of tree annual diameter increment was based on specific species fits.

Key words: random effects, fixed effects, diameter increment, second growth forest

INTRODUCTION

Peninsular Malaysia is quite fortunate to be endowed with a sizable proportion of land covered with natural dipterocarp forest. In 1998, 5.86 million ha of the land area was still covered with forest. About 2.83 million ha has been classified as productive forest under the Permanent Forest Estate, which is to be managed in a sustainable manner (Thang 2000). Most of the productive forest is confined to the hilly areas and has been managed under the Selective Management System (SMS) since the late 1970's. SMS is a polycyclic system with a cutting cycle of 30 years. Trees larger than a certain specified diameter limit were harvested, with the diameter limit based on a pre-harvest inventory. The success of the SMS to sustain timber production for the next cut is dependent on the stocking, growth and survival of healthy intermediate-sized trees. Assessment of the potential success of the SMS requires the development of a growth prediction system that provides the basis for yield regulation of second growth hill dipterocarp forest. One of the key components to be incorporated in the growth prediction system is tree basal area or dbh increment model.

Three basic model types have been used in predicting diameter growth; linear, intrinsically linear (non-linear that can be linearized through logarithmic transformation) and intrinsically non-linear forms (Hann and Larsen, 1991). Ong and Kleine (1995) and Chai and LeMay (1993) applied a linear model for diameter growth in mixed inland and in swampy mixed dipterocarp forest of east Malaysia, respectively. Wan Razali (1986) tested both linear and non-linear models for mixed dipterocarp forest in Peninsular Malaysia and found that the linear model performed best.

In the tropics, two types of growth response have been predicted: diameter growth (Wan Razali and Rustagi, 1986; Vanclay 1991; Chai and LeMay, 1993) and basal area growth (Ong and Kleine 1995). Wan Razali (1986) compared the

relative performance of diameter increment and basal area increment for five major groups of species in mixed dipterocarp forests of Peninsular Malaysia and identified diameter increment as more appropriate; conversely, Ong and Kleine (1995) found that basal area increment gave a better fit to the data. Alder (1995) also favored basal area increment over diameter increment since it permitted a linear form with a higher coefficient of determination. Ultimately, any differences in goodness-of-fit may be due to the difference in error structure and implied functional relationship rather than the inherent superiority of one model over the other (Furnival 1961, Vanclay 1994).

Several diameter increment functions have taken into account the tree and stand attributes for major trees in mixed dipterocarp forest in Malaysia. Wan Razali's (1986) model applies to regenerated forests in Peninsular Malaysia, Ong's and Kleine's (1995) model applies to logged-over forests in Sabah, and Chai's and LeMay's (1993) model applies to peat swamp forest of Sarawak. To date only the model developed by Ong and Kleine (1995) has been incorporated into a forest growth simulation model for the purpose of yield regulation.

The specific attributes serving as predictor variables in these models depend on the type of forest and resolution of predictions. Vanclay (1995) argued that many variables used in plantation growth models have little relevance to tropical rainforests. Variables such as top height and crown ratio which are common in diameter increment models for even-aged stands, are difficult to measure in tropical rainforests. Among the most common variables are tree diameter, tree competition, stand density and site quality (Vanclay 1994; Ong and Kleine 1995). Wan Razali (1986) found that addition of the previous growth measurement into the diameter increment equation resulted in significant improvement in the predictive ability of the model for regenerated mixed dipterocarp forest, but this variable is seldom available from operational surveys done with temporary plots. Chai and LeMay (1993) tested various measures of competition from other trees, time elapsed and growth potential as reflected by initial dbh. Vanclay (1991) predicted diameter

growth from tree diameter, basal area of larger trees, total stand basal area, and combination of site quality and tree diameter in Queensland tropical rainforest.

One approach to selecting the most appropriate predictor variables relies on established growth models. Another approach is selection by statistical procedure such as all-subsets regression analysis (Draper and Smith 1981; Hann and Larsen 1991). The first approach may exclude potential predictor variables during model development since different species and stand conditions may warrant different predictors; and the second may not provide an optimal solution with respect to biologically meaningful predictor variables in the final model. However, the latter approach does provide a set of alternative models that can be prioritized or modified to ensure biologically rational behavior. In general, empirical tree growth models should include common tree and stand attributes, although the combination of these attributes can be species-specific for mixed-species, multi-cohort stands.

Tropical mixed forests are generally characterized by a large number of species with diverse growth habits. The huge challenge in this forest has been construction of 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, or even lack of identification to the species level. In ecological studies of tropical rainforests, tree species are typically classified based on their ecological functions. For example, Manokaran and Swaine (1994) classified trees as emergent, main canopy, under-story, pioneer or late-seral species. Wan Razali (1986) developed growth equations for five commercial species groupings recognized by the Forestry Department of Peninsular Malaysia. The commercial groups included dipterocarps and four groups of non-dipterocarps: light hardwoods, medium hardwoods, heavy hardwoods and other miscellaneous species. The grouping of species in this latter case was necessitated by the difficulty of providing sufficient depth and range of data necessary to model species individually. Chai and LeMay (1993) tested three levels of species resolution, including individual species, two groups of species

(light-demanding and shade-tolerant) and all species combined. They found that modeling at the individual species level resulted in only a slight gain in predictive power compared with lumping all species. No real gain was obtained by recognizing two groups versus one group. 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 behavior 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 re-measurements available for each species. This method provided better predictive power than other models based on subjectively formed groups.

As with many other tropical forests, hill dipterocarp forests of Peninsular Malaysia contained many species with insufficient data for reliable parameter estimation. Grouping of species has been the common approach to fitting prediction equations (Vanclay 1995). The hypothesis explored here is that diameter growth of individual trees in hill dipterocarp forest can be gainfully modeled by treating species as a random effect in a mixed-effect, non-linear regression model. This approach offers several advantages:

- a) the model form is common to all species, with slight perturbations to each parameter arising from the random species effect;
- b) all data are used in a single estimation algorithm;
- c) non-linear mixed-effects models allow the random species effect to enter in either a linear or non-linear manner, and

- d) in a simulation context varying levels of resolution with respect to species or species grouping can be accommodated by the same equation

Past applications of mixed-effects modeling in tropical forestry are apparently few. Mixed-effects models are primarily used to describe relationships between a response variable and predictor variables when the data are grouped according to one or more classification factors (Pinheiro and Bates 2000). In the temperate regions, several applications of mixed-effects models have been tested. Biging (1985) presented a linear random-coefficients model for site index curves to account for between-tree differences in individual tree height growth. Data from individual trees were combined to estimate parameters for a sigmoid height growth model. In stem profile modeling, Tassissa and Burkhart (1998) applied a random-effects model in which a random effect was attributed to trees with multiple measurements. They also accounted for the correlation among observations within a single stem, achieving improvements over techniques that ignore auto correlation. In dealing with a nested data structure in modeling tree growth, Penner et al. (1995) accommodated random effects at varying levels of nesting. Hokka et al. (1997) found a significant random effect of stands on individual tree growth. Hokka and Groot (1999) further achieved a reduction in the random error variances in their individual tree growth model when they accounted for spatial and temporal correlation among observations. Gregoire et al. (1995) applied a linear mixed-effects model to three sets of growth data, accounting for the covariance between repeated measurements as well as random plot effects. Maguire et al. (1999) applied a mixed-effects non-linear model to estimate maximum branch diameter at a given depth into crown, allowing for a random effect from individual trees.

The overall objective of this study was to develop a model for predicting individual tree annual dbh increment in second growth hill dipterocarp forest. An appropriate model form was identified, with selection of dependent and independent variables suitable for predicting individual tree diameter growth.

Fixed-effects and random-effects models were then evaluated with respect to the appropriateness of treating species as random effects.

METHODS

Field Sites

The modeling data set was obtained from experimental cutting plots established in second-growth hill dipterocarp forest. The study site is located at Compartment 5a, Tekam Forest Reserve, State of Pahang (N 3° 55 ' - N 4° 10 ', E 102° 20 ' - E 102° 43') (Figure 17). The annual precipitation ranges from 2765 to 2980 mm, while the average temperature is between 24 °C to 29 °C (Dale, 1963). The monthly rainfall distribution in 1987 to 1989 was bimodal with maxima occurring in April and November (Baharuddin et al. 1995). The terrain is low and undulating but becomes increasingly steep with a rise in elevation, especially near ridge-tops. The species composition before felling was not known. However, an earlier report by Wan Razali and Roslan (1983) in Compartment 5b, a nearby area, indicated that some of the most common commercial trees in the area were *Shorea curtisii*, *S. pauciflora*, *S. leprosula*, *Agathis borneensis*, *Koompassia malaccensis*, *Dipterocarpus* sp., *S. parvifolia*, *Dyera costulata*, *Anisoptera* sp., and *S. macroptera*. The average number of trees greater than 10 cm dbh per hectare is 514 trees and the predominance of Seraya (*S. curtisii*) on the ridge-crest is an indication of the hill dipterocarp forest.

The main objective of the experiment was to determine the response of residual trees to different logging methods and cutting limits. The two logging methods were conventional tractor logging and high-lead yarding. Three cutting limits were prescribed at 45 cm dbh, 52 cm dbh and 62 cm dbh. All trees above the cutting limit were designated for harvest. The design and layout of the experimental

plots are shown in Table 17 and Figure 18, respectively. The experimental design can be considered a 2 x 3 factorial experiment. Each experimental unit is a one-hectare plot, that is 100 m x 100 m. Three replicates in each treatment combination (logging method and cutting limits) were established, one each on the ridge-top or upper slope, middle-slope and valley bottom. Each plot was subdivided into 25, 20 m x 20 m subplots and given a unique number beginning with 1 and ending with 25. The sampling units for the determination of the stand competition and density were the 20 m X 20 m plots. All values were converted to a per hectare basis.

Data description

The first measurement was conducted immediately after logging in 1979. Subsequently, the plots were measured in 1980, 1981, 1982, 1983, 1984, 1985, 1987, 1989, 1994 and 1999. Several plots however, were not measured in 1980, 1984 and 1985.

In each subplot, all trees greater than 10 cm dbh were measured and tagged sequentially with a unique number, beginning with 1 for the first recorded tree. In the re-measurement, trees reaching 10 cm in dbh were given a new number subsequent to the last numbered tree in the subplot. By having a unique plot number, subplot number and tree number, each tree identity was preserved. Missing values in any tree diameter series were linearly interpolated, and small negative increments were converted to zero. A maximum annual increment of 3 cm was set as an acceptable growth limit for trees in the second growth forest, as it is uncommon for trees to grow greater than 3 cm especially among the non-pioneer species. All data were used in the analysis.

Identification of all trees to the species level is a laborious task and was not within the framework of the research project. In the hill dipterocarp forest of Seraya-Ridge sub-type, species richness can reach over 487 species in a 6-ha plot

(Niiyama et al. 1999). Experienced field foresters identified species by their local names, which are the preferred vernacular names recommended by Wyatt-Smith and Kochumen (1999). However, each local name may represent a different taxonomic level, ranging from species or genus to family. For example, a tree identified as Keruing (*Dipterocarpus* spp.) and one identified as Keruing gombang (*Dipterocarpus cornutus*) were kept as two separate local names. A total of 207 local names were recorded. The local name was the taxonomic unit on which random effects were based, but they will be referred to hereafter as species. The species vary considerably in rate of growth and maximum dbh (Table 18), and the silvicultural treatments achieved a wide range in residual stand density (Table 19).

Table 17: Design of the experimental plots at Tekam Forest Reserve, Peninsular Malaysia.

Logging Method	Cutting limits	Replicates number
Highlead yarding	45 cm dbh	1,2,3
	52 cm dbh	4,5,6
	60 cm dbh	7,8,9
Tractor logging	45 cm dbh	10,11,12
	52 cm dbh	13,14,15
	60 cm dbh	16,17,18

Each replicates is 1-hectare plot (100 m x 100 m)

Figure 17: Forest map and location of study site

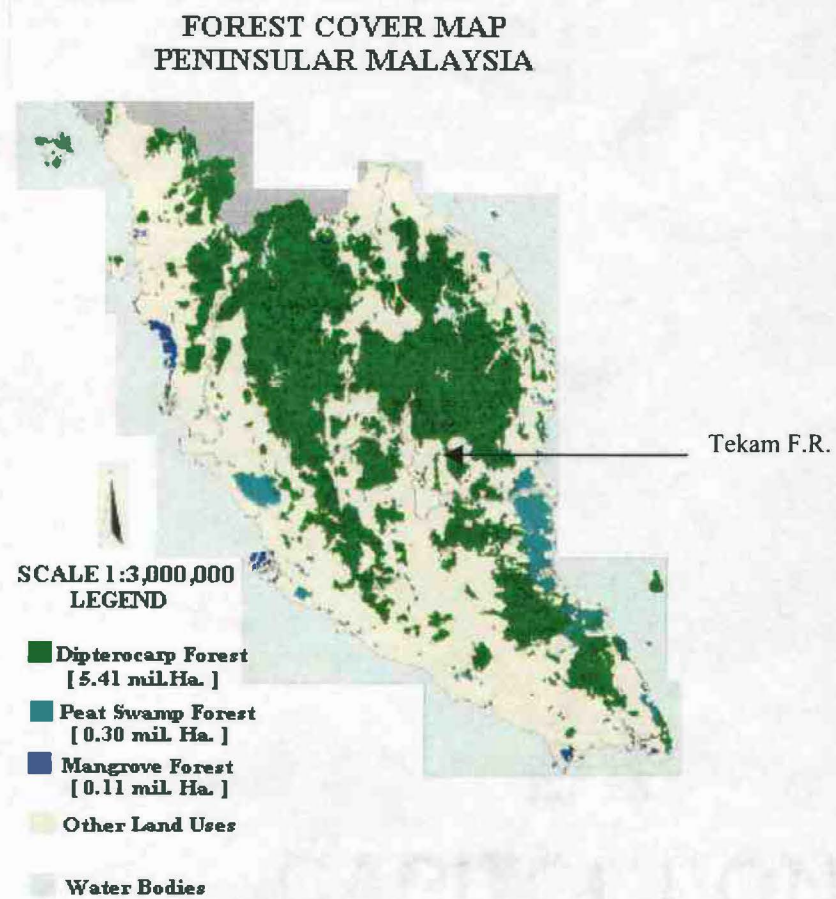
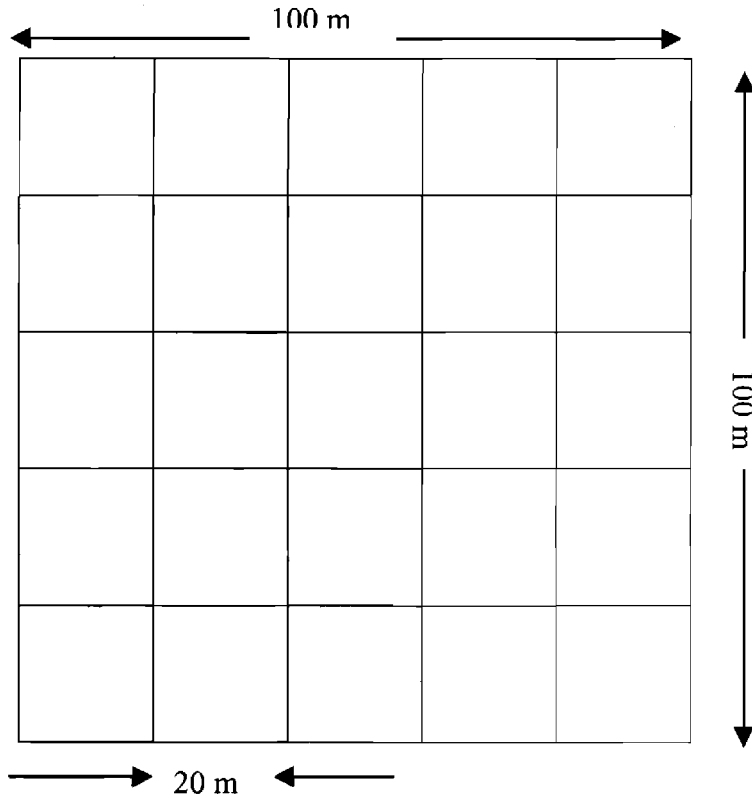


Figure 18: Layout of 1-hectare experimental plots with divisions of 25 sub-plots



Data Structure

The independent variables can be grouped into tree-level attributes and stand-level attributes. The tree-level attributes were categorized into tree size, tree position and tree competition variables, while the stand-level attributes were categorized into stand density and average size. Tree size variables included:

dbh = diameter at 1.3 m

$\ln(\text{dbh})$ = natural logarithm of dbh

sdi1.6: individual tree contribution to sdi1.6 (stand density index) = $(\text{dbh}_i/25.4)^{1.6}$

sdi2.0: individual tree contribution to sdi2.0 = $(dbh_i/25.4)^{2.0}$

sdi2.6: individual tree contribution to sdi2.6 = $(dbh_i/25.4)^{2.6}$

sdi1.6= Stand density index assuming maximum size-density slope of 1.6

sdi2.0= Stand density index assuming maximum size-density slope of 2.0

sdi2.6= Stand density index assuming maximum size-density slope of 2.6

where sdi K = $(dbh_i/25.4)^K$ where K= 1.6, 2.0 or 2.6

The calculation of sdi1.6, sdi2.0 and sdi2.6 was based on the maximum size- density concept (Reineke 1993, Long and Daniel 1990) and the contribution of individual trees to total stand sdi (Reineke 1933, Long and Daniel 1990). The exponent represents the slope of the maximum size-density line. A higher maximum size-density slope confers a greater value if $dbh > 25.4$ but a lower value if $dbh < 25.4$. When $dbh = 25.4$, 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 forest of Peninsular Malaysia (see Chapter 2).

Tree competition/position variables were:

osdi1.6= Stand density index of trees larger (by dbh) than the subject tree,
assuming a maximum size-density slope of 1.6

osdi2.0= Stand density index of trees larger (by dbh) than the subject tree,
assuming a maximum size-density slope of 2.0

osdi2.6= Stand density index of trees larger (by dbh) than the subject tree,
assuming a maximum size-density slope of 2.6

Table 2: Summary statistics for species with > 200 observations in experimental plots at Tekam Forest Reserve

Species by local names	Number of observations	Mean DBH increment \pm SD	Mean dbh (cm)	Maximum dbh (cm)	Overtopping sdi (min – max)
(A)					
Meranti tembaga	512	0.86 \pm 0.63	29.2	70.5	0-699
Meranti sarang punai	664	0.71 \pm 0.63	32.8	117.0	0-951
Meranti melantai	664	0.69 \pm 0.50	24.5	93.0	0-846
(B)					
Mertas	605	0.30 \pm 0.28	26.8	92.0	0-841
Perah	2208	0.30 \pm 0.29	25.3	80.3	0-957
Kelat	7794	0.30 \pm 0.31	19.3	72.0	0-1225
(C)					
Ludai	342	1.16 \pm 0.92	18.8	37.2	0-731
Kubin	623	1.01 \pm 0.66	15.2	31.2	0-730
Mempening	939	0.89 \pm 0.59	22.0	55.3	0-825
(D)					
Nipis kulit	327	0.17 \pm 0.21	13.9	36.4	0-994
Kayu arang	401	0.21 \pm 0.23	16.2	38.7	69.9-1128
Langsat hutan	259	0.24 \pm 0.24	18.1	45.0	44.1-773

(A) – Fast growing trees with maximum DBH > 70 cm

(B) – Slow growing trees with maximum DBH > 70 cm

(C) – Fast growing trees with maximum DBH < 60 cm

(D) – Slow growing trees with maximum DBH < 60 cm

Table 3: Summary statistics for selected stand-level attributes of experimental plots at Tekam Forest Reserve, all species combined

Variables	Min	Mean	Median	Max
Trees per hectare	25.0	484	475	1020
Maximum DBH	10.2	57.8	53.2	200.0
Quadratic mean DBH	10.2	25.7	24.9	58.4
Basal area per hectare	0.20	25.9	23.7	92.7
Stand density index *	5.81	433	434	1240

* based on maximum size-density slope of 1.6

reldq= Ratio of dbh of the subject tree to quadratic mean dbh
 reldmax= Ratio of dbh of the subject tree to maximum dbh
 rosdi1.6= Ratio of subject tree osdi1.6 to the stand density index, sdi1.6
 rosdi2.0= Ratio of subject tree osdi2.0 to the stand density index, sdi2.0
 rosdi2.6= Ratio of subject tree osdi2.6 to the stand density index, sdi2.6

Stand-level density and average size variables included:

tph= Trees per hectare

dmax= Maximum stand dbh

Dq= Quadratic mean dbh

DA= Arithmetic mean dbh

Basal area of the stand and overtopping basal area were excluded from all-subsets regression analysis because sdi with $K=2$ is a linear function of basal area. Therefore, sdi2.0 and osdi2.0 in a linear model are equivalent to stand basal area and overtopping basal area, respectively.

The natural logarithm of each variable was considered in the selection process in addition to the untransformed variable. An all-subsets regression analysis was performed on each of the three data sets. The first data set included only the stand density index components for which the maximum size-density slope is 1.6, plus other variables. Similarly, the second and third data set included only the stand density index for maximum size-density slope of 2.0 and 2.6, respectively. A fixed maximum size-density slope for stand density index calculation is an even-aged concept (Reineke 1933). Sterba and Monserud (1993) showed that the maximum size-density lines in uneven-aged stands of primarily Douglas-fir were influenced by stand structure and habitat type. Application of the

maximum size-density or the limiting density concept has not been explored in mixed-species tropical forest. However, some evidence of a potential limiting density has been observed from two long-term permanent 2-ha plots established in a primary lowland and hill dipterocarp forest in Peninsular Malaysia (Chapter 2). Manokaran (1998) found that stand basal area of primary lowland dipterocarp forest and a regenerating lowland dipterocarp forest was quite similar, although both stands had marked differences in stand structure and tree density. In the regenerating forests, the scarcity of larger trees were compensated for by the large number of small trees. Since the existence and level of any limiting density in hill dipterocarp forest has not been firmly established, the effects of sdi calculated from alternative maximum size-density slopes were tested for their relevance to dbh increment.

Selection of Basic Model

The basic diameter or basal area growth model was;

$$\log (y) = \alpha_0 + \alpha_1 x + \alpha_2 \log (x) + \varepsilon \quad [7]$$

(linear model)

or

$$y = \exp (\alpha_0 + \alpha_1 x + \alpha_2 \ln(x)) \cdot \varepsilon^* \quad [8]$$

(intrinsically linear model)

where

y is the tree diameter or basal area increment

x is initial tree diameter or basal area

$\varepsilon \sim N(0, \sigma^2)$

α_0, α_1 and α_2 are parameters to be estimated from the data

The response variable was calculated as the difference between size at the start of the growth period and its size at the end of the growth period, divided by the time period between measurements; that is, the response variable was periodic annual increment for each individual tree. The basic model has the desirable property of allowing for a peaking behavior and a long-term asymptotic approach to zero. The long right hand tail on the increment curve function accommodates the very slight but continued increment accrued by large trees (Vanclay 1994).

Linear and non-linear models for both basal area and diameter increment were tested to determine the most appropriate model form for the Tekam data. Both unweighted and weighted forms of the non-linear model were tested.

In addition to a low Furnival's Index, the parameter estimates for β_1 and β_2 should be negative and positive, respectively, to produce a growth pattern that initially increases, reaches a peak, and then declines as the tree matures.

Selection of Tree Stand Predictor Variables

A group of promising models was selected from all-subsets results on the basis of the Cp statistic and adjusted R^2 (Draper and Smith 1981). Both dbh and $\ln(\text{dbh})$ were forced into each model to retain the basic model form.

The selection of final predictor variables was based on three basic elements, i.e., tree size, competition effect and stand density. The criteria for model selection included a requirement that signs on parameter estimates reflect logical biological behavior. For example, a negative parameter for dbh and positive parameter for $\ln(\text{dbh})$ implies a peaking behavior over dbh and diameter growth that becomes asymptotic to zero as dbh increases beyond the peak. Negative parameters for sdi and osdi imply that an increase in dbh increment can be expected with a reduction

in stand density or overtopping trees. Secondly, a smaller number of variables is preferred among models with similar adjusted R^2 and Cp statistics.

Species as Fixed-Effects

Species fixed-effect models were tested for two species levels: 1) ecological functional groups, and 2) vernacular names. The ecological functional groups were recognized as pioneers, late seral, emergents, main canopy, and understory species as described by Manokaran and Swaine (1994) and Wyatt-Smith and Kochumen (1999). *Pioneers* are short-lived tree species that require a gap for germination and establishment and show rapid growth, but they are extremely light demanding and shade-intolerant. *Late-seral* species are light-demanding but quite tolerant to shade and are prominent at later stages of succession. The species can persist to form part of the mature forest. *Emergents* are mature phase long-lived species growing above the main canopy of primary forest, usually with spreading crowns. *Main canopy* species are also characteristic of the mature phase and are relatively long lived species that form the main canopy of primary forest, growing to heights of 20-30 m. *Understorey* species are mature-phase, shade-tolerants forming the lower strata of the the primary forest with maximum height below 20. The mature phase species consist of light-demanding light hardwood species (e.g., *Shorea leprosula*) or shade-tolerant heavy hardwood species (e.g., *Neobalanocarpus hemii*) at the early stage of tree growth.

The basic linear fixed-effects model was:

$$Y_j = X_j \alpha + \epsilon_j \quad [9]$$

$$\epsilon_j \sim N(0, \sigma^2)$$

where Y_j is the observed natural logarithm of dbh increment, X_j is a $1 \times p$ vector of predictor variables for observation j including species grouping as a set of

indicator variables, vector α represents the p fixed effects, and σ^2 is the variance of the error term, ε_j .

For example, using growth model [8] and assuming q species in the model:

$$\ln(\text{dbh}_j) = \alpha_0 + \alpha_1 \text{dbh}_j + \alpha_2 \ln(\text{dbh}_j) + \sum \alpha_{i+2} \cdot \text{sp}_i + \varepsilon_j \quad [10]$$

where

$$\text{sp}_i = \begin{cases} 1 & \text{if species group } i \\ 0 & \text{otherwise} \end{cases}$$

$i=1,2,3,\dots,q$

Species as Random-Effects

In mixed-effects models, the random effect is assumed to be a random draw from some population of possible coefficients (Littell et al. 1996). Hence, the regression model for each species is assumed to be a random deviation from some population of regression models.

The linear mixed-effects model was initially formulated as:

$$Y_i = X_i \alpha + \delta_i + \varepsilon_i \quad [11]$$

where y_i is a $n_i \times 1$ vector of observations for species group i , X_i is a $n_i \times p$ matrix of predictor variables for species group i , δ_i is a $n_i \times 1$ vector of the random species effect, ε_i is a $n_i \times 1$ vector of random errors,

$$i = 1, 2, 3, \dots, q$$

q = number of species groups

n_i = number of observations in species group i

$$\delta_i \sim N(0, \sigma^2_b B),$$

$$\varepsilon_j \sim N(0, \sigma^2_w W)$$

The parameters in the model are the p fixed-effects represented in vector α , the random effects in vectors δ_i and ε_i and the $n_i \times n_i$ covariance matrices $\sigma_b^2 B$ and $\sigma_w^2 W$ for the random species effects. In this application, B and W are assumed to be the $n_i \times n_i$ identity matrices with σ_b^2 and σ_w^2 on the diagonals, respectively, X_i is a $n_i \times 3$ matrix with columns containing 1, dbh, and $\ln(\text{dbh})$. Parameters were estimated by the restricted maximum likelihood method (Prinheiro and Bates 2000). The significance of the fixed-effects was assessed by approximate t-tests.

Model [11] allows for the intercept of the equation to vary by species. However, species was also expected to influence the slope of at least some of the basic predictor variables, so an expanded model was formulated as follows:

$$Y_i = X_i \alpha + Z_i \delta_i + \varepsilon_i \quad [12]$$

where X_i , α and ε_i are as above.

$Z_i = n_i \times p$ matrix of predictor variables

$\delta_i = p \times 1$ vector of random species effects

Finally, the non-linear forms of the diameter growth models were also assessed for their performance relative to the corresponding linear models.

$$Y_i = f(X_i, \alpha, Z_i, \delta_i) + \varepsilon_i \quad [13]$$

where $f(\cdot)$ is a nonlinear function depending on known covariates, and other symbols are as defined earlier.

Likelihood ratio statistic were computed to compare between reduced and full models:

$$2\ln(L_F/L_R) = 2[\ln(L_F) - \ln(L_R)]$$

where L_F is the likelihood of the full model and L_R is the likelihood of the reduced model. If P_F is the number of parameters to be estimated in the full model and P_R the number of parameters in the reduced model, then the asymptotic distribution of the likelihood ratio statistic, under the null hypothesis that the reduced model is adequate, is χ^2 with $P_F - P_R$ degrees of freedom (Pinheiro and Bates 2000). The Akaike Information Criterion (AIC) was also computed to compare models (Pinheiro and Bates 2000).

Assessment of Models

The validity of the underlying distributional assumptions for the selected linear random coefficients model was checked before making inferences. Two basic assumptions were considered (Pinheiro and Bates, 2000):

- a) within-species errors are independent and identically distributed, follow a normal distribution with mean zero and constant variance σ and are independent of random effects.
- b) the random effects are normally distributed, with mean zero and constant variance σ^2_b and are independent for different groups.

The validity of each assumption was assessed by residuals plot, fitted values, and estimated random effects. The residuals were plotted on predictor variables to check for bias across different levels of each predictor variable. Graphical analyses of species, as both a fixed and random effect, were also performed. Graphical comparison was only made on data grouped by vernacular names. The sign of covariance in the random effects model indicated the variability among responses between species or across species. Lindsey (1999)¹ indicated that

¹ Page 90

a negative covariance implies more variability among responses within each unit than across units. Such cases occur when a study is based on very similar units.

Although there were almost certainly within-plot correlations among trees and within-tree correlations across time, they were not accounted for in the analysis, in part because computation of these multiple random effects became prohibitive in nonlinear mixed-effects models.

Assessment of Growth Behavior

The biological behavior of diameter growth as implied by the final model was examined for three species within each functional group in Table 18: emergent (3); main canopy (4); and pioneers (2). The first three species, Meranti tembaga (*Shorea leprosula leprosula*), Meranti sarang punai (*S. parvifolia*) and Meranti melantai (*S. macroptera*) are the light-demanding mature-phase emergents, also classified as the Light Hardwood timber group. They are the fastest growing mature species in the data set. The next three species were among the slowest growing mature phase species, namely Kelat (mostly *Syzygium* sp), Perah (*Elateriospermum tapos*) and Mertas (*Ctenolophon parvifolius*). The pioneers were represented by Kubin (*Macaranga gigantea*) and Ludai (*Sapium baccatum*), and Mempening (*Lithocarpus* sp) was the fourth main canopy species. Our main aim was to demonstrate the dbh increment pattern of different species or group of species over different predictor variables.

RESULTS

Basic Model

The selected basic equation was an unweighted logarithmically transformed linear model with dbh increment as the dependent variable. This model had the lowest FI value (Table 20) and signs on parameter estimates met biological expectations (Table 21).

$$\ln(\text{dinc}+0.01) = \alpha_0 + \alpha_1 * \text{dbh} + \alpha_2 * \ln(\text{dbh}) + \varepsilon \quad [14]$$

Table 20: Results of the multiple linear regression and non-linear regression for model [7] and [8]

a) Dbh increment model

Model	weight	FI	rmse
$\ln(\text{dinc}+0.01)=b_0 + b_1\text{dbh} + b_2\ln(\text{dbh})$	1	0.28	1.541
$\text{dinc}+0.01=b_0 \text{dbh}^{b_2} \exp(b_1\text{dbh})$	1	0.44	0.436
“	dbh^{-1}	0.91	0.207
“	dbh^{-2}	1.97	0.101
“	dbh^{-3}	4.36	0.050

b) Basal area increment model

Model	weight	FI	rmse
$\ln(\text{bag}+0.01)=b_0 + b_1\text{bat} + b_2\ln(\text{bat})$	1	0.32	2.770
$\text{bag}+0.01=b_0 \text{bat}^{b_2} \exp(b_1\text{bat})$	1	2.91	22.820
“	bat^{-1}	91.50	41.400
“	bat^{-2}	3530	92.060
“	bat^{-3}	155000	232.600

Similar findings have been reported by Wan Razali (1988). He compared relative performance of diameter versus basal area increment in models for mixed dipterocarp forest with Furnival's (1961) index of fit. Diameter increment was concluded to be a more appropriate dependent variable for modeling individual tree growth in mixed tropical rainforest (Wan Razali 1988). The residual standard error of the selected model [14] was 1.54. Both predictor variables were highly significant (Table 21).

Table 21: Parameter estimates and standard errors for model [14]

Parameter	Estimate	Standard error	P _{value}
α_0	-4.0209	0.0849	<0.0001
α_1	-0.0450	0.0013	<0.0001
α_2	1.1140	0.0373	<0.0001

Tree and Stand Predictor Variables

Eleven of the fourteen models selected were based on predictors assuming a maximum size-density slope of 1.6. Among the most common variables selected were sdit1.6, osdi1.6, sdi1.6 and dmax and (Table 22). Osdi1.6 and sdi1.6 were expected to be negatively correlated with dbh increment, while dmax to be positively correlated. Only the model with dbh, ln(dbh), dmax, osdi1.6, and log(sdi1.6) as predictor variables seemed to produce rational behavior.

The following four-parameter equation was selected as the best linear model for predicting overall tree dbh increment of second growth hill dipterocarp forest:

$$\ln(\text{dinc}+0.01) = \alpha_0 + \alpha_1 \text{dbh} + \alpha_2 \ln(\text{dbh}) + \alpha_3 \text{osdi1.6} + \alpha_4 \log(\text{sdi1.6}) + \alpha_5 \text{dmax} \quad [15]$$

All predictor variables were significant with $P = 0.0001$, and the rmse was 1.52. All predictor variables showed expected signs on parameter estimates, i.e., negative for α_1 , α_3 and α_4 , and positive for α_2 and α_5 (Table 23).

Table 22: Results of all-subsets regression. Characters in bold represent the selected model

Variable	Cp	p	Adjusted R^2
dbh, log(dbh), log(sdi1.6)	343	3	3.94
dbh, log(dbh), log(sdi1.6)	349	3	3.93
dbh, log(dbh), osdi1.6, log(sdi1.6)	297	4	3.86
dbh, log(dbh), dmax, log(sdi2.6)	279	4	4.03
dbh, log(dbh), dmax, log(sdi2.0)	284	5	4.02
dbh, log(dbh), dmax, osdi1.6, log(sdi1.6)	184	5	4.20
dbh, log(dbh), log(dmax), osdi1.6, log(sdi1.6)	243	5	4.11
dbh, log(dbh), dmax, sdi1.6, osdi1.6, log(sdi1.6)	139	6	4.28
dbh, log(dbh), dmax, log(dmax) ^{ns} , osdi1.6, log(sdi1.6)	157	6	4.25
dbh, log(dbh), dmax, sdi1.6, osdi1.6, log(sdi1.6), reldmax ^{ns}	121	7	4.31
dbh, log(dbh), dmax, log(dmax), sdi1.6, osdi1.6, log(sdi1.6)	122	7	4.31

n.s. : not significant at 5% probability level

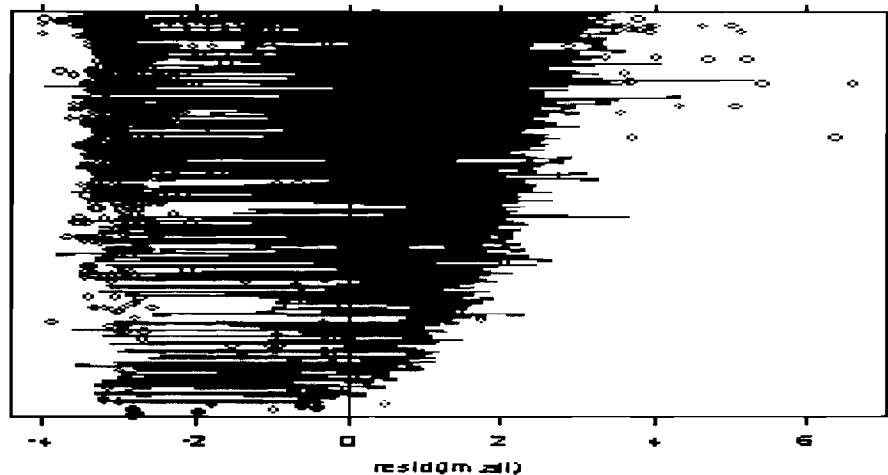
p is the number of co-variates in the model

Table 23: Parameter estimates and standard errors for linear fixed-effects model [15] based on selected predictor variables in all-subset regression analysis

Parameter	Estimate	Standard error	P_{value}
α_0	-1.949	0.138	<0.0001
α_1	-0.046	0.001	<0.0001
α_2	0.942	0.040	<0.0001
α_3	-0.001	0.000	<0.0001
α_4	-0.242	0.028	<0.0001
α_5	0.004	0.000	<0.0001

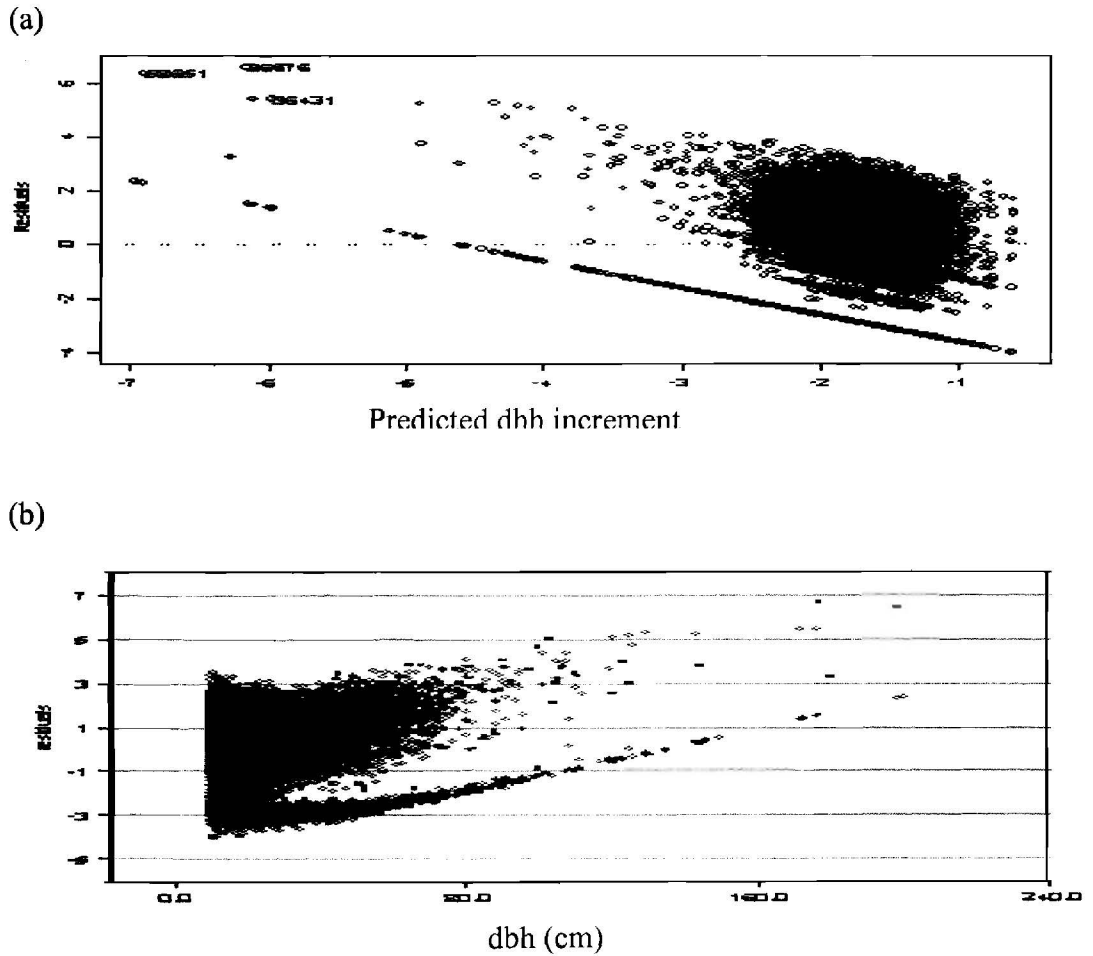
Residuals from model [15] plotted by vernacular name indicated that the residuals for a given species were not centered around zero mean and exhibited non-constant variance (Figure 19).

Figure 19: Residuals from model [15] plotted on species defined by vernacular names

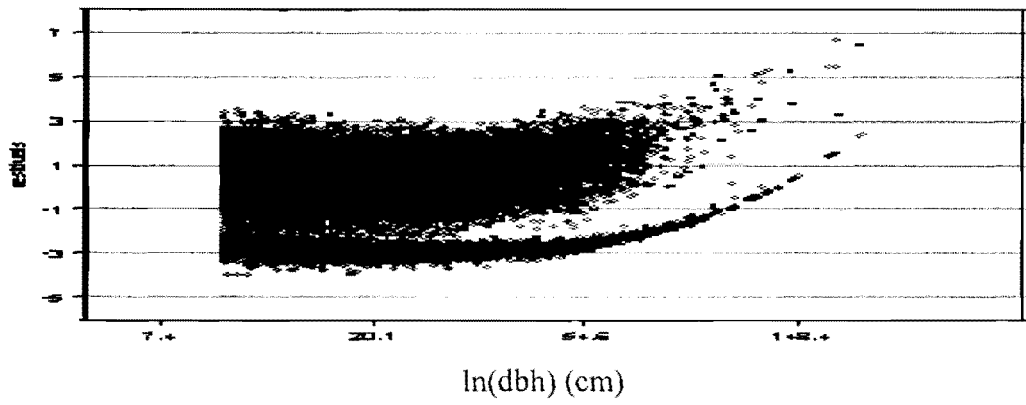


The scatter plots of residual versus predicted dbh increment (Figure 20a) indicated an obvious segregation of dbh increment equal to zero and greater than zero. Similar trends were also shown in all scatter plots of residuals against other predictor variables. The residuals pattern indicated an upward curve for larger trees, indicated some bias in prediction of diameter increment for larger trees (Figure 20b-c). Specifically, large trees exhibited higher than expected growth rate. The scatter plot of residuals on overtopping stand density index, stand density index and maximum stand dbh indicated no biases (Figure 20d-f).

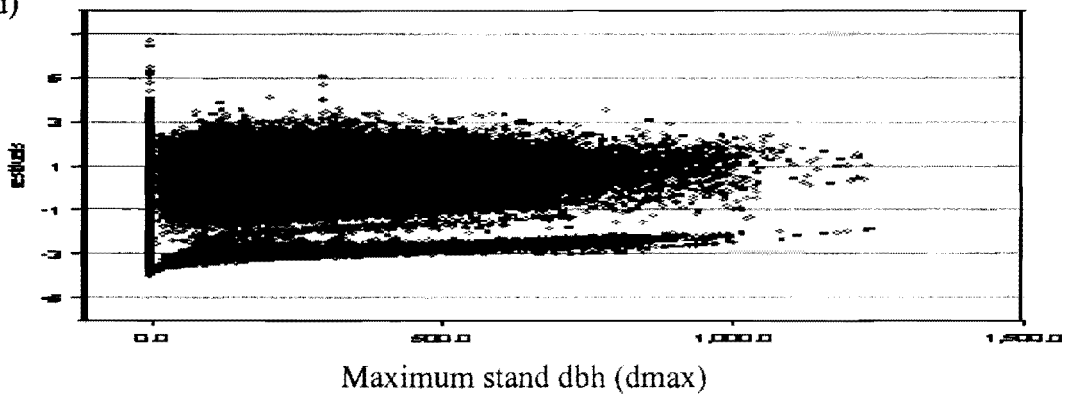
Figure 20: Scatter plots of residuals versus (a) predicted dbh increment, (b) dbh, (c) natural logarithm of dbh, (d) overtopping stand density index (osdi1.6), (e) stand density index (sdi1.6), and (f) maximum stand dbh (dmax) for model [15]



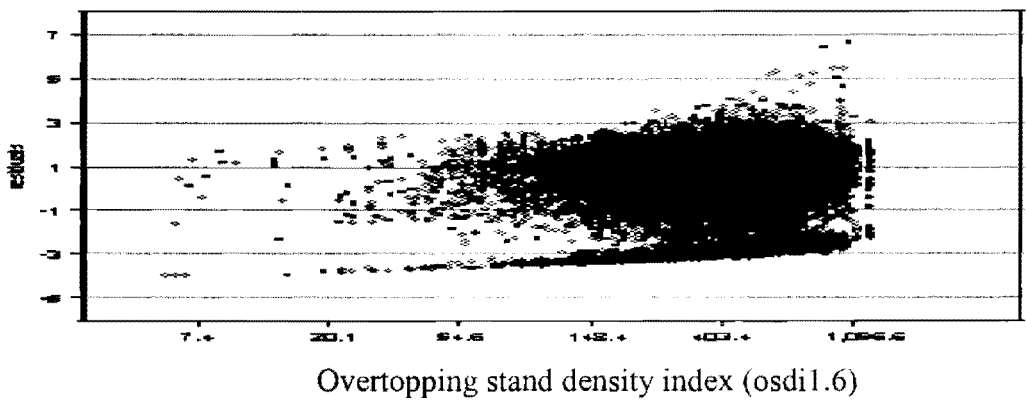
(c)



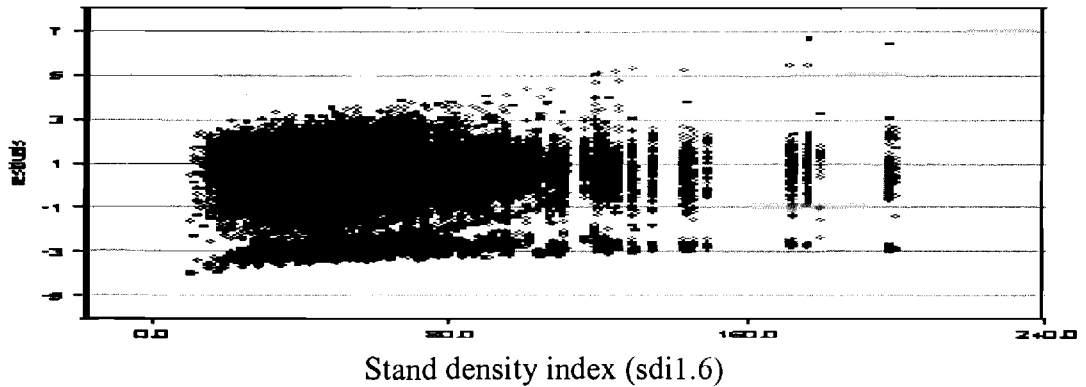
(d)



(e)



(f)



Species as Fixed-Effects

Two levels of species classifications were tested: 1) by ecological groupings and b) by vernacular names. Based on model [9], the general equation accounting for fixed species effects by ecological grouping was:

$$\ln(\text{dinc}+0.01) = \alpha_0 + \alpha_1 \text{dbh} + \alpha_2 \ln(\text{dbh}) + \alpha_3 \text{sdi1.6} + \alpha_4 \log(\text{sdi1.6}) + \alpha_5 \text{dmax} \\ + \alpha_6 \text{sp}_1 + \alpha_7 \text{sp}_2 + \alpha_8 \text{sp}_3 + \alpha_9 \text{sp}_4 + \alpha_{10} \text{sp}_5 + \varepsilon \quad [16]$$

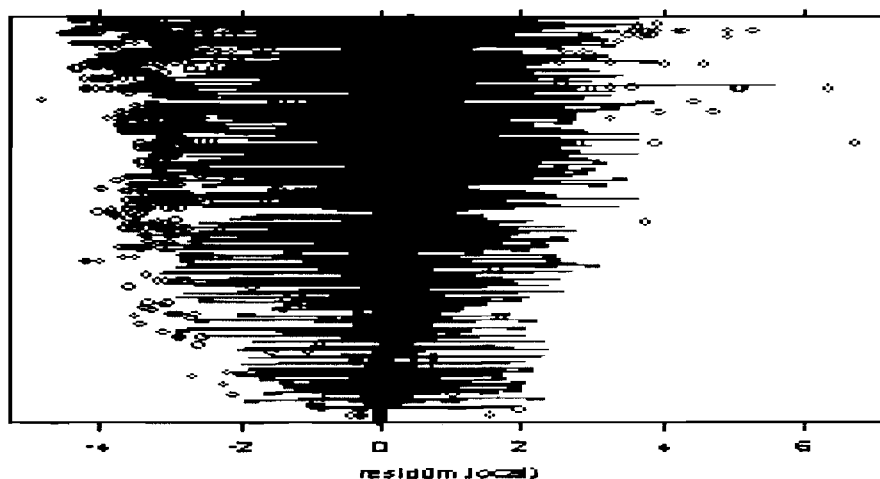
where sp_k is the ecological group indicator variable.

The number of parameter estimates increases linearly with the number of indicator variables, so 5 parameters are added for ecological groupings and 206 parameters are added for vernacular names. All predictor variables showed the expected sign on parameter estimates for both species levels, i.e., negative for α_1 , α_3 and α_4 , and positive for α_2 and α_5 (Table 24). The parameter estimates of the fixed effects predictor variables for model [15] (Table 23) and model [16] (Table 24)

effects predictor variables for model [15] (Table 23) and model [16] (Table 24) were similar. The residual standard error was slightly reduced for ecological groupings from 1.52 to 1.51, and further reduction was obtained when vernacular names were introduced ($rmse=1.46$).

The residuals (Figure 21) from model [16] indicated a slight bias in the positive direction for most vernacular names, but the residual distributions were more closely centered around zero relative to model [15]. However, treating species as a fixed effect causes an increase of 206 in number of parameters to be estimated in model [16].

Figure 21: Residual plots corresponding to model [16] predicted dbh increment, by vernacular names



Residual distribution of model [16] over predicted dbh increment and all predictor variables was similar to model [15]. The plot of residuals versus predicted dbh increment (Figure 22a) indicated an obvious segregation of observations with increment equal to zero and greater than zero. Similar trends were also observed for residuals plotted against predictor variables. The scatter plot of residuals against dbh and natural logarithm of dbh indicated positive bias for larger trees (Figure 22 b-c). The scatter plot of residuals over overtopping stand density index, stand

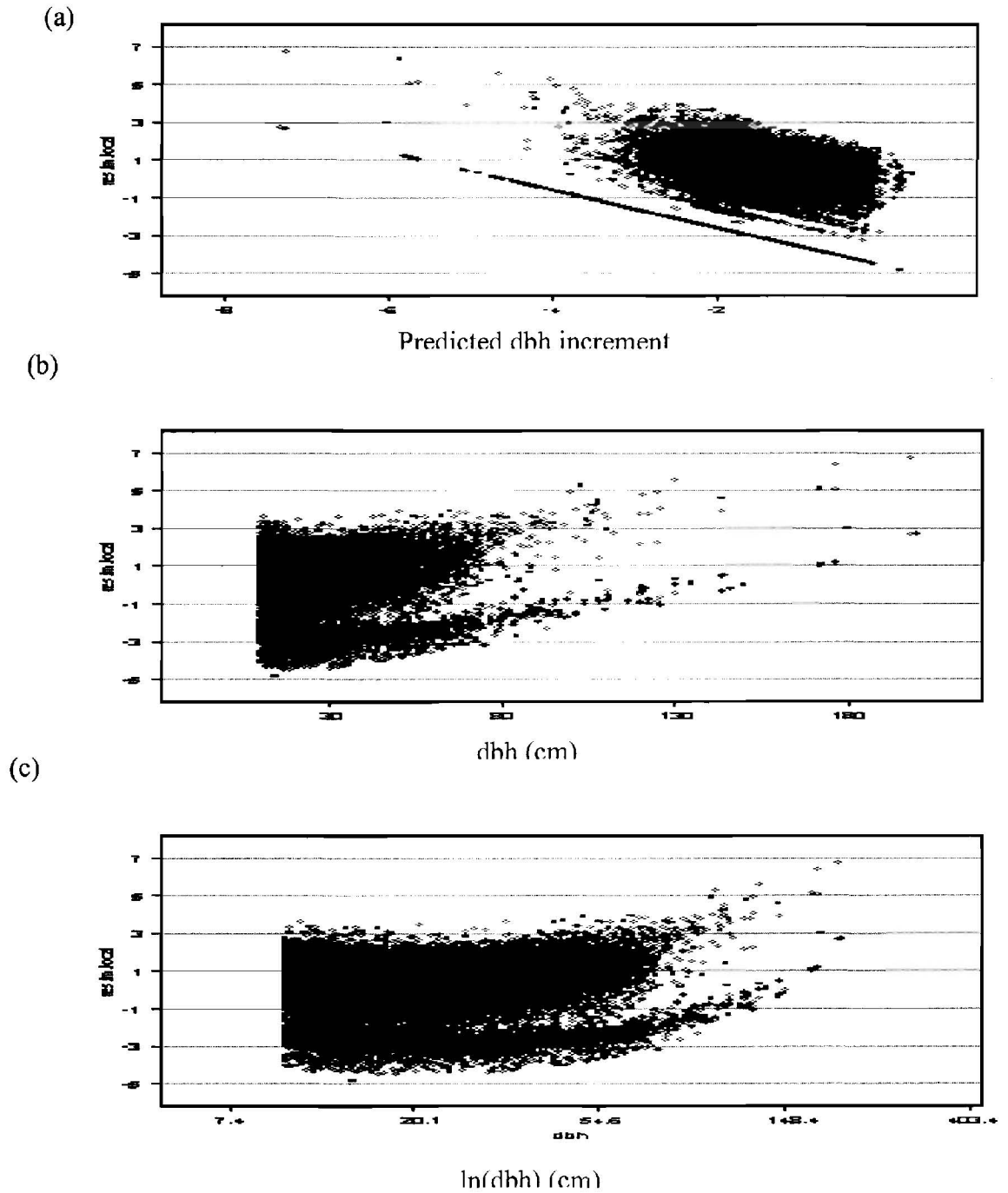
(Figure 22 d-f). The segregation of residuals is less obvious in model [16] as compare to model [15] after accounting for species effects.

Table 24: Results of linear model on selected predictor variables with fixed effects for ecological grouping; and vernacular names for model [16]

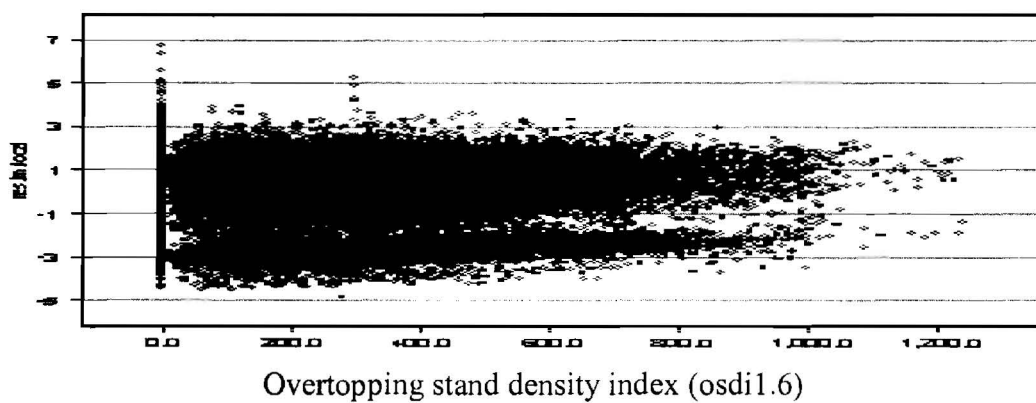
Parameter	Estimate	Standard error	P _{value}
<u>Ecological groupings</u>			
α_0	-1.938	0.136	<0.0001
α_1	-0.049	0.001	<0.0001
α_2	0.984	0.040	<0.0001
α_3	-0.001	0.000	<0.0001
α_4	-0.224	0.028	<0.0001
α_5	0.004	0.000	<0.0001
α_6	0.257	0.035	<0.0001
α_7	-0.187	0.012	<0.0001
α_8	0.134	0.012	<0.0001
α_9	-0.171	0.006	<0.0001
α_{10}	-0.070	0.007	<0.0001
<u>Vernacular names</u>			
α_0	-2.240	0.138	<0.0001
α_1	-0.051	0.005	<0.0001
α_2	1.006	-0.013	<0.0001
α_3	-0.001	-0.011	<0.0001
α_4	-0.231	0.018	<0.0001
α_5	0.005	0.007	<0.0001

There were 206 indicator variables for vernacular names and was not shown in the Table 24.

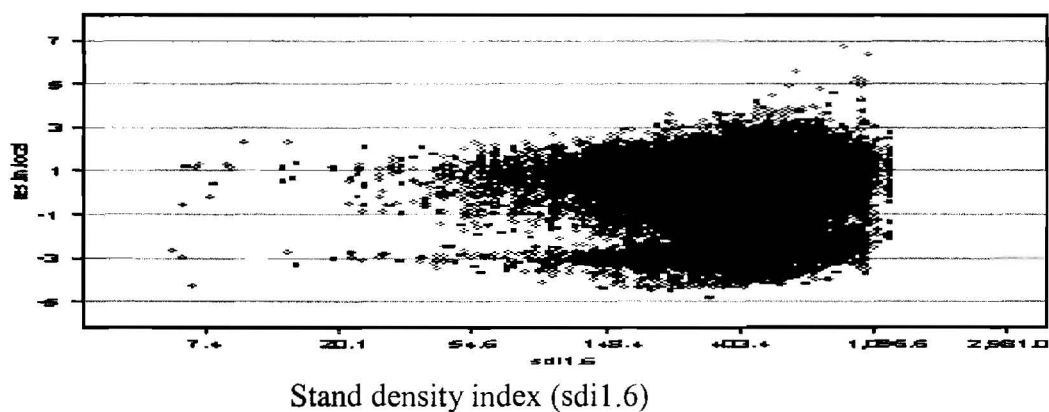
Figure 22: Scatter plots of residuals versus (a) predicted dbh increment, (b) dbh, (c) natural logarithm of dbh, (d) overtopping stand density index (osdi1.6), (e) stand density index (sdi1.6), and (f) maximum stand dbh (dmax) based on model [16]



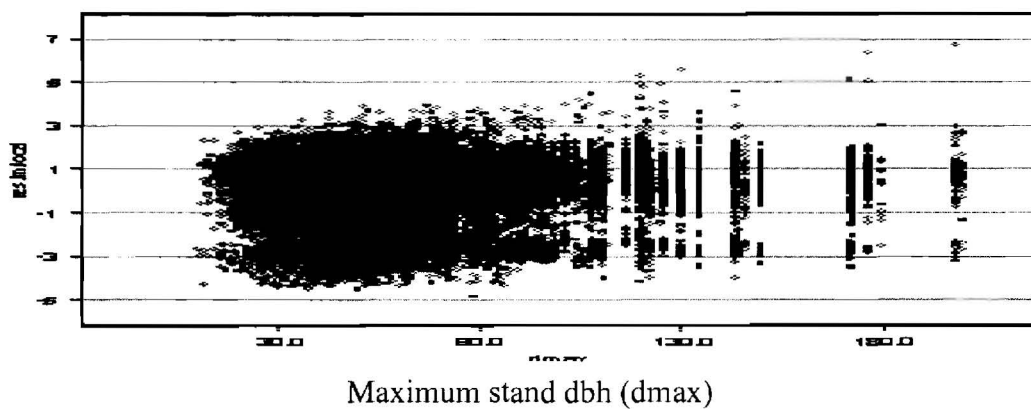
(d)



(e)



(f)



Species Random Effects

Two types of linear random species effects were tested:

- a) linear model with random species effects on intercept only,

$$\ln(\text{dinc}+0.01)_{ij} = \alpha_0 + \alpha_1 \text{dbh}_{ij} + \alpha_2 \log(\text{dbh}_{ij}) + \alpha_3 \text{osdi}1.6 + \alpha_4 \log(\text{sdi}1.6) + \alpha_5 \text{dmax} + \sum (\delta_i) + \varepsilon \quad [17]$$

- b) linear model with random species effects on both the intercept and the slopes of tree size predictor variables

$$\ln(\text{dinc}+0.01)_{ij} = \alpha_0 + \alpha_1 \text{dbh}_{ij} + \alpha_2 \log(\text{dbh}_{ij}) + \alpha_3 \text{osdi}1.6 + \alpha_4 \log(\text{sdi}1.6) + \alpha_5 \text{dmax} + \sum (\delta_{1i} + \delta_{2i} \text{dbh}_{ij} + \delta_{3i} \log(\text{dbh}_{ij})) \quad [18]$$

where $\delta_{1i} \sim N(0, \sigma^2_{B1})$

$$\delta_{2i} \sim N(0, \sigma^2_{B2})$$

$$\delta_{3i} \sim N(0, \sigma^2_{B3})$$

Models for both ecological groupings and species indicated that parameter estimates were similar to the fixed-effects model, except for intercepts, which were higher for species than for ecological grouping (Table 25). The variance of the random species effect was also larger for species than ecological grouping. The positive sign on the variance of random species effects indicated that there was more variability between species than within species for both groupings.

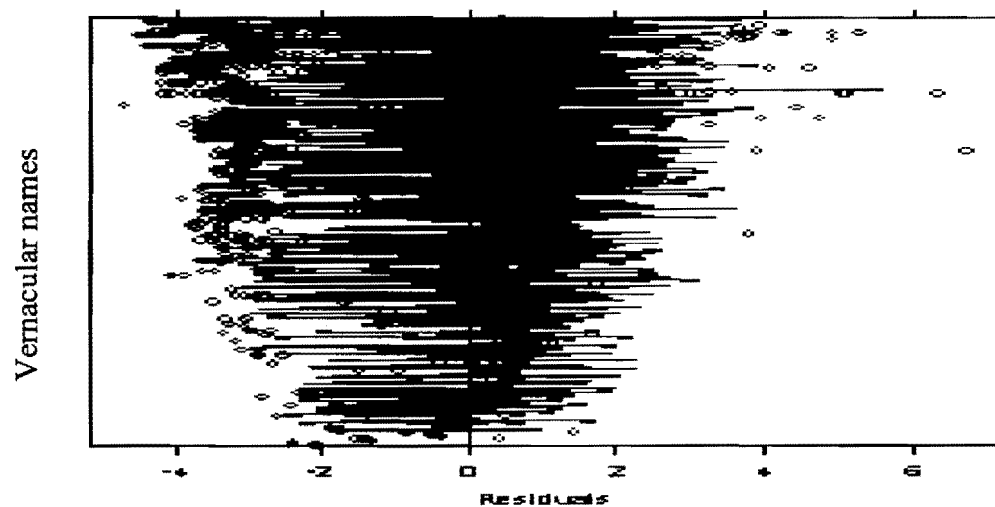
Table 25: Parameter estimates and standard errors for the linear random species effects model [17]

Parameter	Ecological groupings		Vernacular names	
	Estimate	Standard Error	Estimate	Standard Error
α_0	-1.939	-0.247	-2.137	0.143
α_1	-0.045	0.001	-0.050	0.001
α_2	0.984	0.040	0.998	0.040
α_3	-0.001	-0.000	-0.001	0.000
α_4	-0.224	-0.028	-0.238	0.027
α_5	0.004	0.000	0.005	0.000
δ_b^2	0.505	-	0.615	-
σ_w^2	1.509	-	1.465	-

The residual plots (Figure 23a-b) corresponding to model [17] indicated a slight positive skew to residuals for most species. The scatter plots of standardized residuals showed an obvious segregation of observations between dbh increment equal to zero and dbh increment greater than zero. The scatter plot of residuals against tree dbh and natural logarithm of dbh produced positive bias when tree dbh exceeded 50 cm (Figure 24b-c). The residuals plotted on osdi1.6 (Figure 24d), sdi1.6 (Figure 24e) and dmax (Figure 24f) did not show similar bias.

Figure 23: Residuals from model [17] : a) plotted on vernacular names, and b) plotted on a normal probability plot

a)



b)

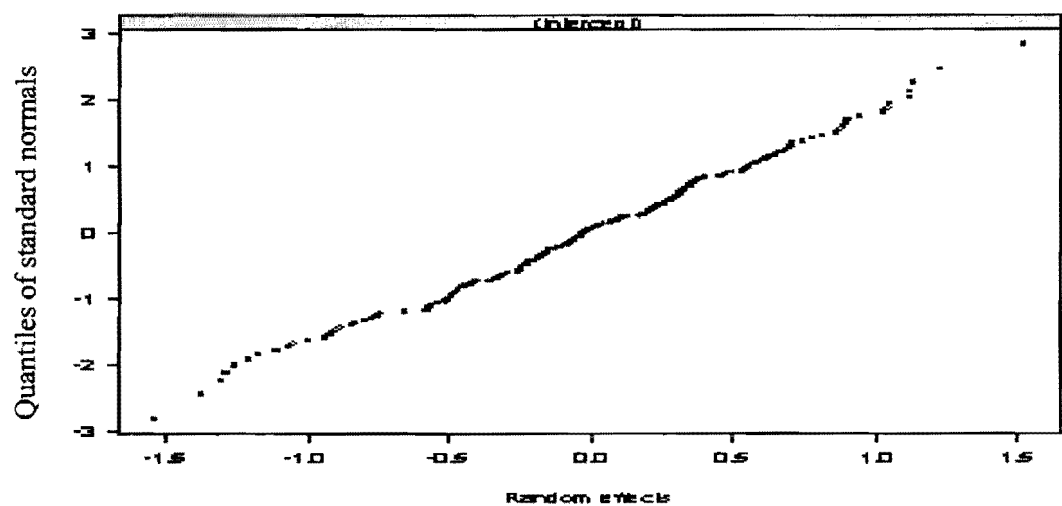
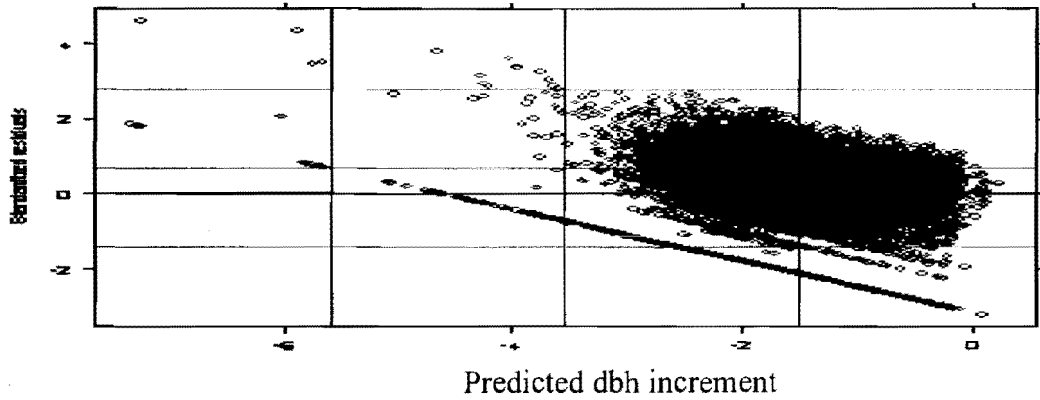
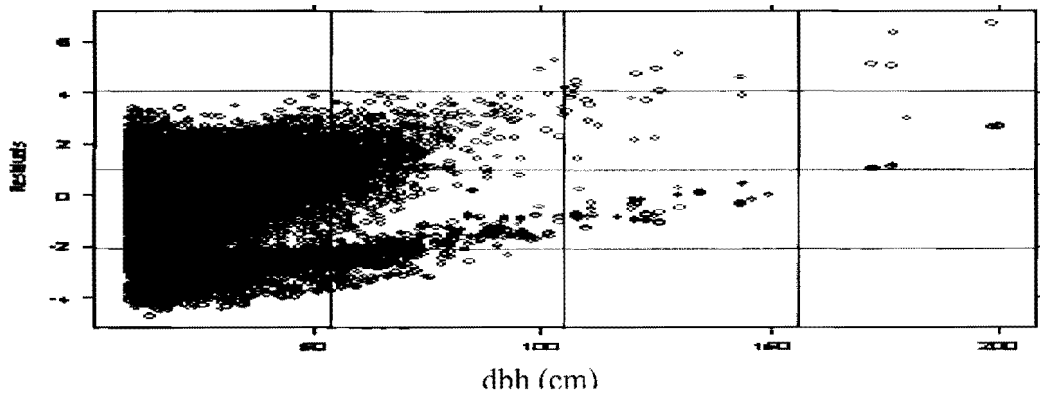


Figure 24: Scatter plot of residuals versus (a) predicted dbh increment, (b) dbh and (c) natural logarithm of dbh, (d) maximum stand dbh (dmax), (e) overtopping stand density index (osdi1.6) and (f) stand density index (sdi1.6) for linear mixed-effects model [17] for all data combined.

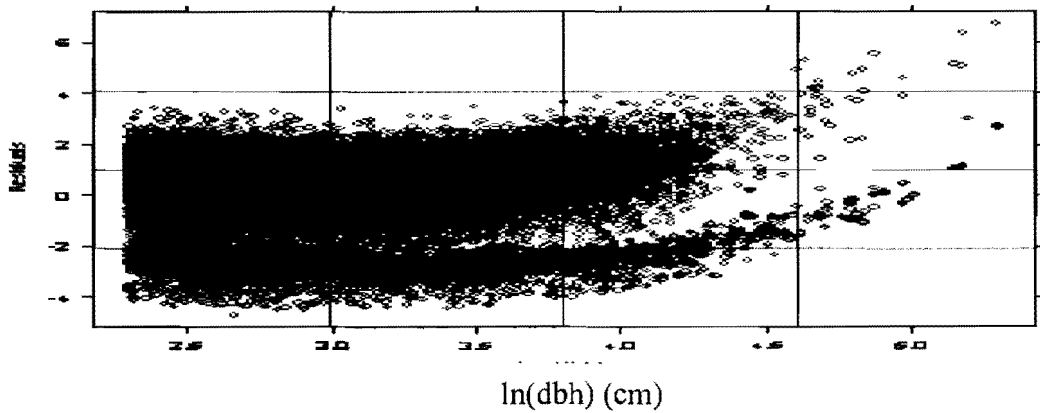
(a)



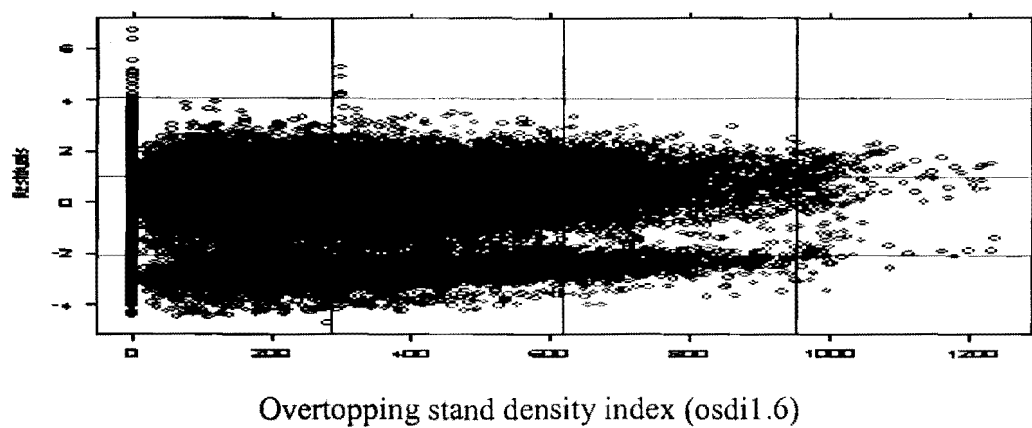
(b)



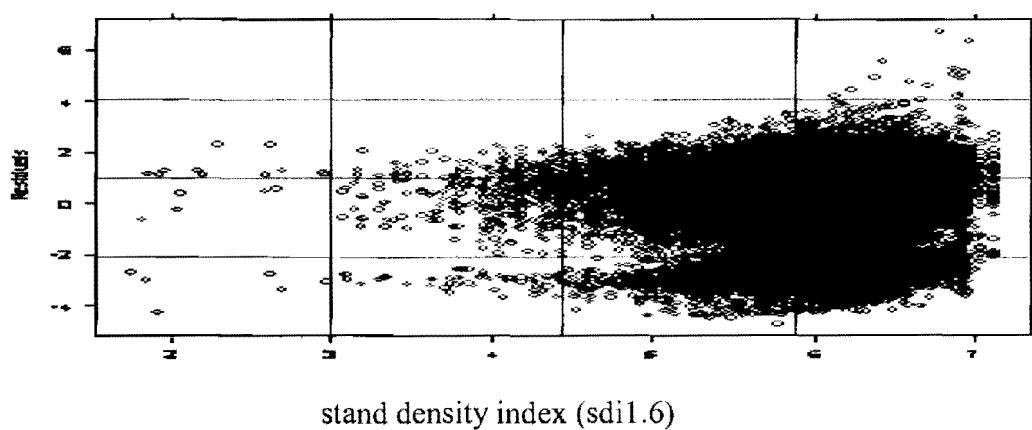
(c)



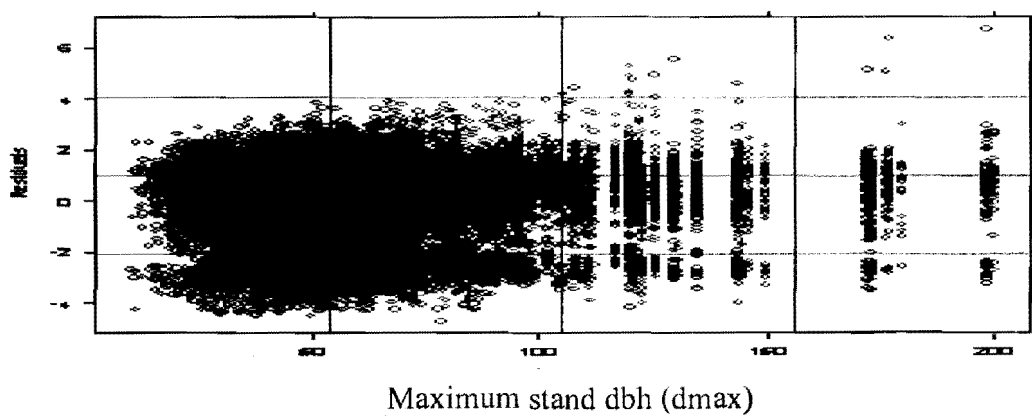
(d)



(e)



(f)



Model [17] was expanded to include random species effects on tree dbh parameters. All parameter estimates showed the expected sign. The relative magnitudes of variances for the random species effects relative to the variance of the unattributable disturbances (σ_w^2) indicates that considerable gain was provided by allowing covariate parameters to vary by species (Table 26).

In ecological groupings a slight reduction in the AIC and rmse from model [16] was observed as compared to model [17]. With vernacular names, a more marked decrease in rmse from fixed effects model [16] to random effects model [17] was observed. The likelihood ratio test comparing model [17] and model [18] indicated that inclusion of random species effects on tree dbh parameters improved the model significantly ($P < 0.0001$, Table 27) for both ecological grouping and vernacular names. However the problem of bias in residual distributions against tree dbh persisted in model [18].

Table 26: Parameter estimates and standard errors for the linear random species effects on tree dbh parameters (model [18])

Parameter	Ecological groupings		Vernacular names	
	Estimate	Standard Error	Estimate	Standard Error
α_0	-1.398	0.527	-1.987	0.308
α_1	-0.049	0.006	-0.051	0.005
α_2	0.777	0.166	0.916	0.128
α_3	-0.001	0.000	-0.001	0.000
α_4	-0.215	0.028	-0.212	0.027
α_5	0.004	0.000	0.005	0.000
σ_{B11}	1.153		2.611	
σ_{B22}	0.010		0.039	
σ_{B33}	0.326		1.116	
σ_w^2	1.509		1.452	

Table 4: Likelihood ratio test comparing model [17] and [18]

Species group	Model	df	AIC	Log-likelihood	Test	Likelihood Ratio	P _{value}
Ecological grouping	17	8	215346	-107665			
	18	13	215303	-107639	5 vs 6	52.90	<0.0001
Vernacular names	17	8	212316	-106150			
	18	13	211693	-105833	5 vs 6	633.21	<0.0001

The apparent bias at high levels of predictor variables suggested the possible need to move from a linear to non-linear mixed model (Figure 25); that is, growth of some large trees were underestimated by the model. The non-linear random coefficient model can be regarded as an extension of the linear random coefficient model in which the conditional expectation of the response given the random effects is allowed to be a nonlinear function of the coefficients (Pinheiro and Bates 2000). The non-linear analysis begins by introducing random species effects on the α_0 , α_1 and α_2 parameters:

$$\text{dinc} = \exp(\alpha_0 + \alpha_1 \text{dbh}_{ij} + \alpha_2 \log(\text{dbh}_{ij}) + \alpha_3 \text{osdi}1.6 + \alpha_4 \log(\text{sdi}1.6) + \alpha_5 \text{dmax} + \sum (\delta_{1i} + \delta_{2i} \text{dbh}_{ij} + \delta_{3i} \log(\text{dbh}_{ij}))) \quad [19]$$

The initial parameter estimates for the non-linear random coefficient model were taken from the fitted log-transformed model [15]. The parameter estimates and standard errors of the fixed effects parameters and variances of random effects from model [19] are shown in Table 28. All fixed-effect parameter estimates had the expected sign for both species levels, i.e., negative for α_1 , α_3 and α_4 , and positive for α_2 and α_5 (Table 28).

The boxplot of residuals by vernacular names showed that mean residuals of species are better centered around zero (Figure 25) than the previous linear random coefficient models (Figure 23a). However non-constant variance of residuals within group is obvious (Figure 25). The assumptions of normality are quite reasonable for both random effects on parameter a_1 and a_2 in model [17] (Figure 26).

No bias was apparent in the plot of residuals versus tree dbh (Figure 27b-c). Based on these finding, the non-linear random coefficient approach was selected to model tree growth. No segregation of residuals between dbh increment equal to zero and greater than zero for all predictor variables (Figure 27d-f). Based on this finding, it was decided to adopt the non-linear random-effects approach to develop the individual tree growth equation.

Table 28: Parameter estimates and standard errors for non-linear random species effects with interaction on tree dbh for model [19]

Parameter	Ecological groupings		Vernacular names	
	Estimate	Standard Error	Estimate	Standard Error
α_0	0.557	0.049	0.540	0.046
α_1	-0.033	0.009	-0.024	0.003
α_2	0.574	0.120	0.481	0.043
α_3	-0.001	0.000	-0.001	0.000
α_4	-0.196	0.014	-0.214	0.012
α_5	0.004	0.000	0.004	0.000
σ_{B11}	-		-	
σ_{B22}	0.022		0.027	
σ_{B33}	0.277		0.275	
σ_w^2	0.417		0.389	

Figure 25: Residuals from model [19] : a) plotted on vernacular names, and b) plotted on a normal probability plot

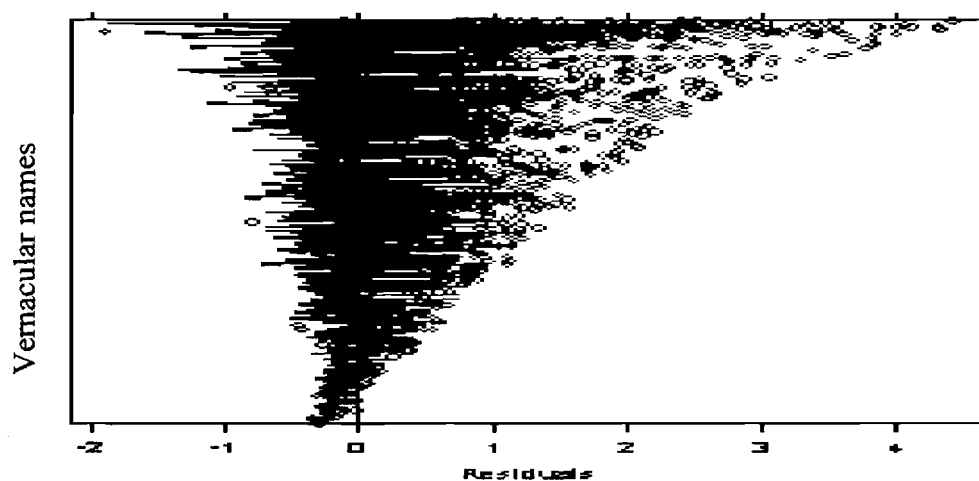


Figure 26: Normal probability plots of random effects on parameter a_1 and a_2 in model [19]. Data was grouped by vernacular names

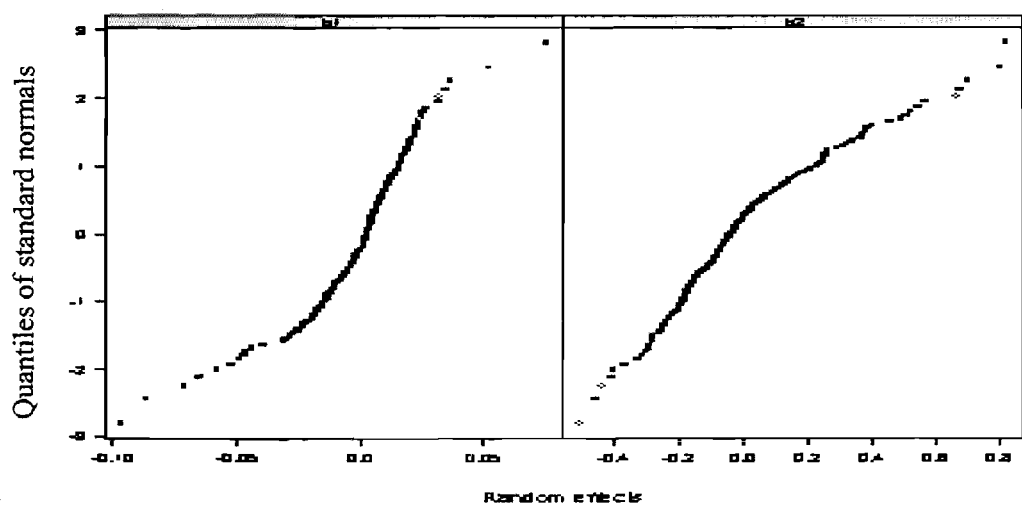
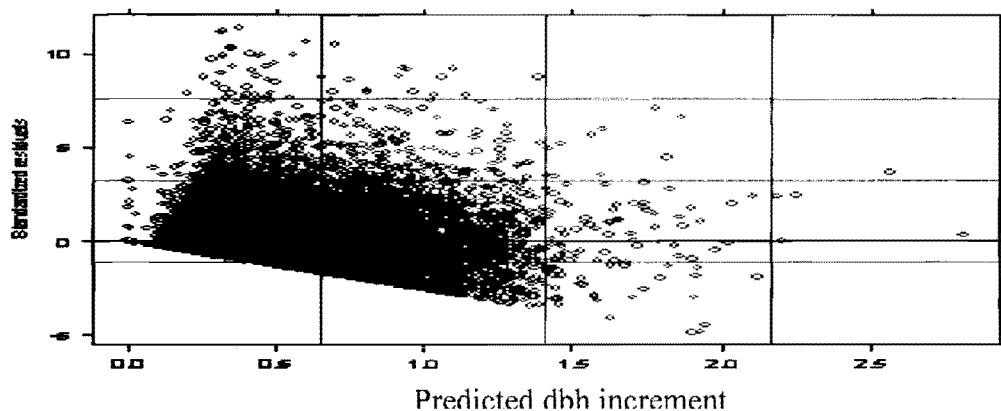
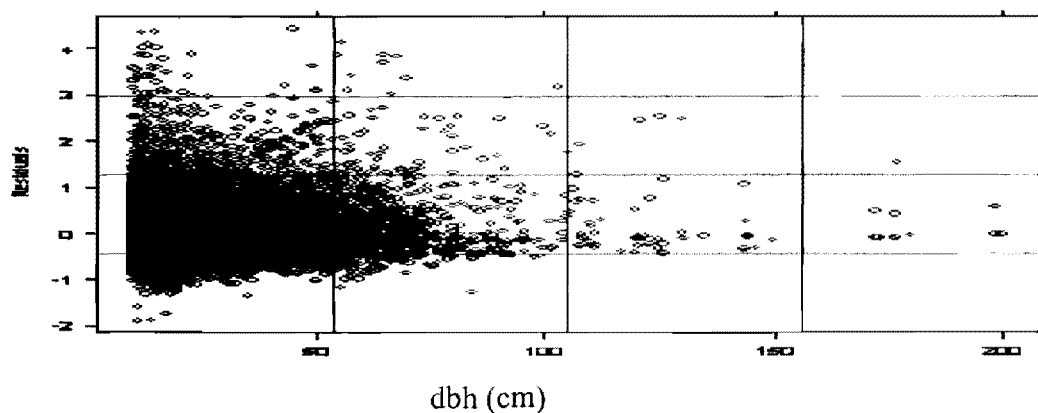


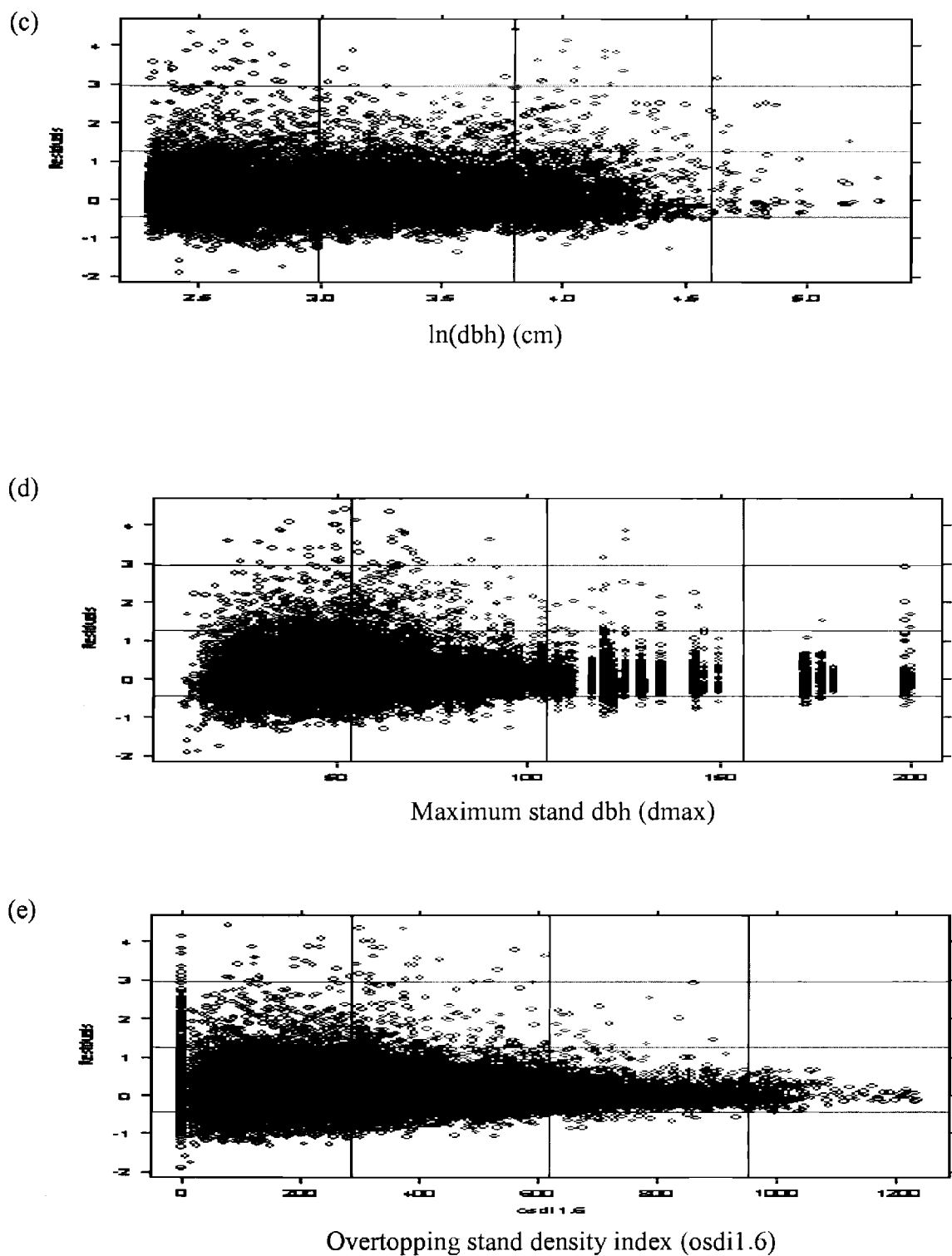
Figure 27: Scatter plot of residuals versus (a) predicted dbh increment, (b) dbh, (c) natural logarithm of dbh, (d) maximum stand dbh (dmax), (e) overtopping stand density index (osdi1.6) and (f) stand density index (sdi1.6) for non-linear random effects model [19]. Data was grouped by vernacular names

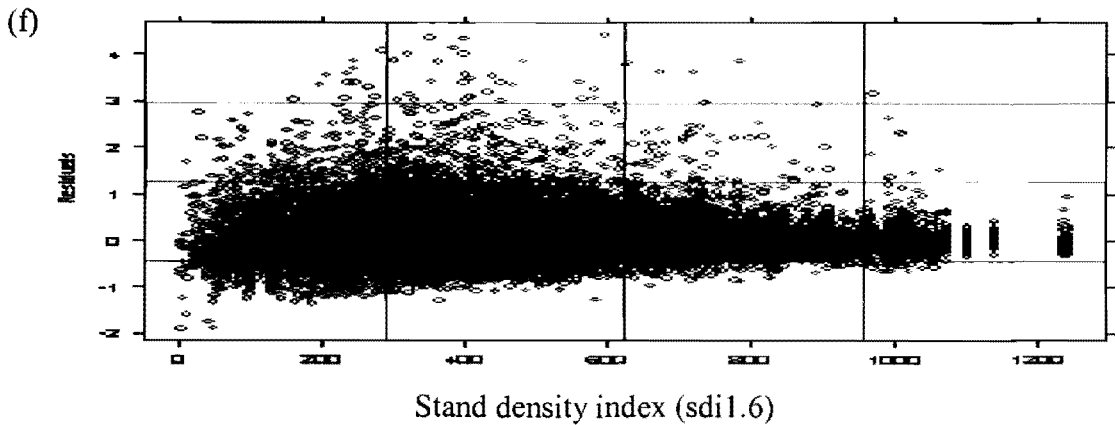
(a)



(b)







The random species effects on the slope of predictor variables were compared to determine the most appropriate model for representing growth behavior of trees in second growth hill dipterocarp forest. The following models were compared:

$$\text{dinc} = \exp(\alpha_0 + \alpha_1 \text{dbh}_{ij} + \alpha_2 \log(\text{dbh}_{ij}) + \alpha_3 \text{osdi1.6} + \alpha_4 \log(\text{sdi1.6}) + \alpha_5 \text{dmax} + \sum (\delta_{1i} + \delta_{2i} \text{dbh}_{ij} + \delta_{3i} \log(\text{dbh}_{ij})) + \epsilon_j) \quad [19]$$

$$\text{dinc} = \exp(\alpha_0 + \alpha_1 \text{dbh}_{ij} + \alpha_2 \log(\text{dbh}_{ij}) + \alpha_3 \text{osdi1.6} + \alpha_4 \log(\text{sdi1.6}) + \alpha_5 \text{dmax} + \sum (\delta_{1i} + \delta_{2i} \text{dbh}_{ij} + \delta_{3i} \log(\text{dbh}_{ij}) + \delta_{4i} \text{osdi1.6} + \delta_{5i} \log(\text{sdi1.6}) +) + \epsilon_j) \quad [20]$$

Model [19] included only tree dbh predictor variables, i.e., dbh and natural logarithm of dbh. Model [20] allowed random species effects on tree dbh, natural logarithm of dbh, osdi1.6 and natural logarithm of sdi1.6. The inclusion of the random species effects on predictor variable parameters allowed the curve for each species to deviate from population average. The parameter estimates and standard error of model [19] and [20] are shown in Table 29.

The inclusion of the additional random effects was tested using the log-likelihood ratio test and by comparing the AIC values between nested models for

the species grouping by vernacular names (Table 30). The log-likelihood test indicated that model [20] performed the best, and it also had the lowest AIC value. The P_{value} for model [20] versus model [19] was highly significant, although only a minor reduction in the rmse from 0.389 in model [19] to 0.387 in model [20] was achieved.

Growth Curve of Trees

All predictor variables in model [21] have random effect terms, except maximum stand dbh (dmax). Graphs of the predicted dbh increment based on the fixed-effects showed the curve of each species relative to population trend. Four graphs of the predicted dbh increment were presented, the first showing predicted dbh increment over tree dbh for “open grown” trees (Figure 28). The open grown trees were estimated under the following assumptions: dbh of the subject tree is equivalent to the maximum dbh (dmax), overtopping stand density index (osdi1.6) equal zero and stand density index (sdi1.6) is equal to tree density index (sdti1.6) multiplied by 25. The latter assumes the subject tree is competing with the equivalent of 24 other trees of the same size. Three trends in the predicted dbh increment curves were observed. Pioneer species reached their peak growth asymptote much earlier than the mature-phase fast-growing species and slow-growing species. Pioneer species showed a sharp increase at the initial stage of size development, but later decreased at a faster rate compared to mature species. Mature species reached the peak growth at a much later stage. The sharp decrease in the growth of pioneer species reflects their need to grow fast to avoid shade (Manokaran and Swaine 1994). The fastest growing pioneer was Ludai (*Sapium bacattum*). Pioneers characteristically have very rapid height growth in youth, and rapid girth growth, at least at first (Whitmore 1984). The slow-growing trees do not show a strongly peaked dbh increment pattern. The deviation of the species-specific dbh increment curve from the mean growth curve illustrates the effect of allowing the influence of dbh and $\ln(\text{dbh})$ to vary by species.

Table 29: Parameter estimates and standard error of non-linear mixed-effects regression analysis of dbh increment based on data grouped by vernacular names

Parameter	Model 19		Model 20	
	Estimates	Standard error	Estimates	Standard error
α_0	0.540	0.046	0.598	0.055
α_1	-0.024	0.003	-0.024	0.003
α_2	0.481	0.043	0.496	0.084
α_3	-0.001	0.000	-0.001	0.000
α_4	-0.214	0.012	-0.243	0.037
α_5	0.004	0.000	0.005	0.000
σ_{b1}	0.027		0.029	
σ_{b2}	0.275		0.741	
σ_{b3}	-		0.001	
σ_{b4}	-		0.329	
σ_{b5}	-		-	
σ	0.389		0.387	

Table 30: Comparing non-linear mixed-effects model fitted by restricted maximum likelihood using likelihood ratio test

Model	df	AIC	logLik	Test	Likelihood ratio	$\alpha = .05$
19	10	56646	-28313			
20	17	56345	-28155	7 vs 8	315.73	<0.0001

The second graph (Figure 29) demonstrates the behavior of predicted dbh increment over the range of dmax when tree dbh equals 30 cm, osdi1.6=100 and sdil.6=450. All species indicated an increase of predicted dbh increment with increase in dmax. The slope of the relationship is constant because there was no

significant effect of species on the influence of d_{max} . Meranti melantai (*S. macroptera*) and Mempening (*Lithocarpus sp*) exhibited the fastest growth among other fast growing trees. However, the rate of change is not large relative to the tree size effects. The influence of d_{max} on tree growth is evident when compared with predicted dbh increment of open grown trees. The ranking of the species for predicted dbh increment at 30 cm dbh changes when competition effects ($osdi1.6$ and $sdi1.6$) were imposed by the equation. Meranti melantai (*Shorea macroptera*) exhibited the fastest growth of all species, although its growth rate was ranked 4th under the open grown condition (Figure 29). Ludai (*Sapium bacattum*) was the fastest growing tree in the open, but was sensitive to competition effects; hence, it ranked 6th under stand conditions.

The third graph (Figure 30) illustrates the behavior of predicted dbh increment over range of tree dbh when $d_{max} = 50$, $osdi1.6=100$ and $sdi1.6=450$. Meranti melantai (*Shorea macroptera*), Meranti tembaga (*Shorea leprosula*), Ludai (*Sapium baccatum*) and Kubin (*Macaranga gigantea*) showed a higher initial dbh increment, but it decreased later at larger size trees. Meranti sarang punai (*Shorea parvifolia*) and Mempening (*Lithocarpus spp.*) were not significantly affected by competition over its range of tree dbh. The slower growing species did not show marked differences in dbh increment over range of tree dbh.

Figure (31) illustrated the effects of competition from below by assigning tree $dbh=d_{max}=25$ cm and $osdi1.6=0$. The negative effect was obvious for the Ludai (*Sapium baccatum*) and Kubin (*Macaranga gigantea*), followed by the mature Meranti sarang punai (*Shorea parvifolia*), Meranti tembaga (*Shorea leprosula*). The slower growing species also showed marked negative effects of increasing competition from below.

Figure 28: Predicting dbh increment of an open grown tree of nine species using the non-linear random coefficients model [20]. The growth curve with only fixed effect is also shown

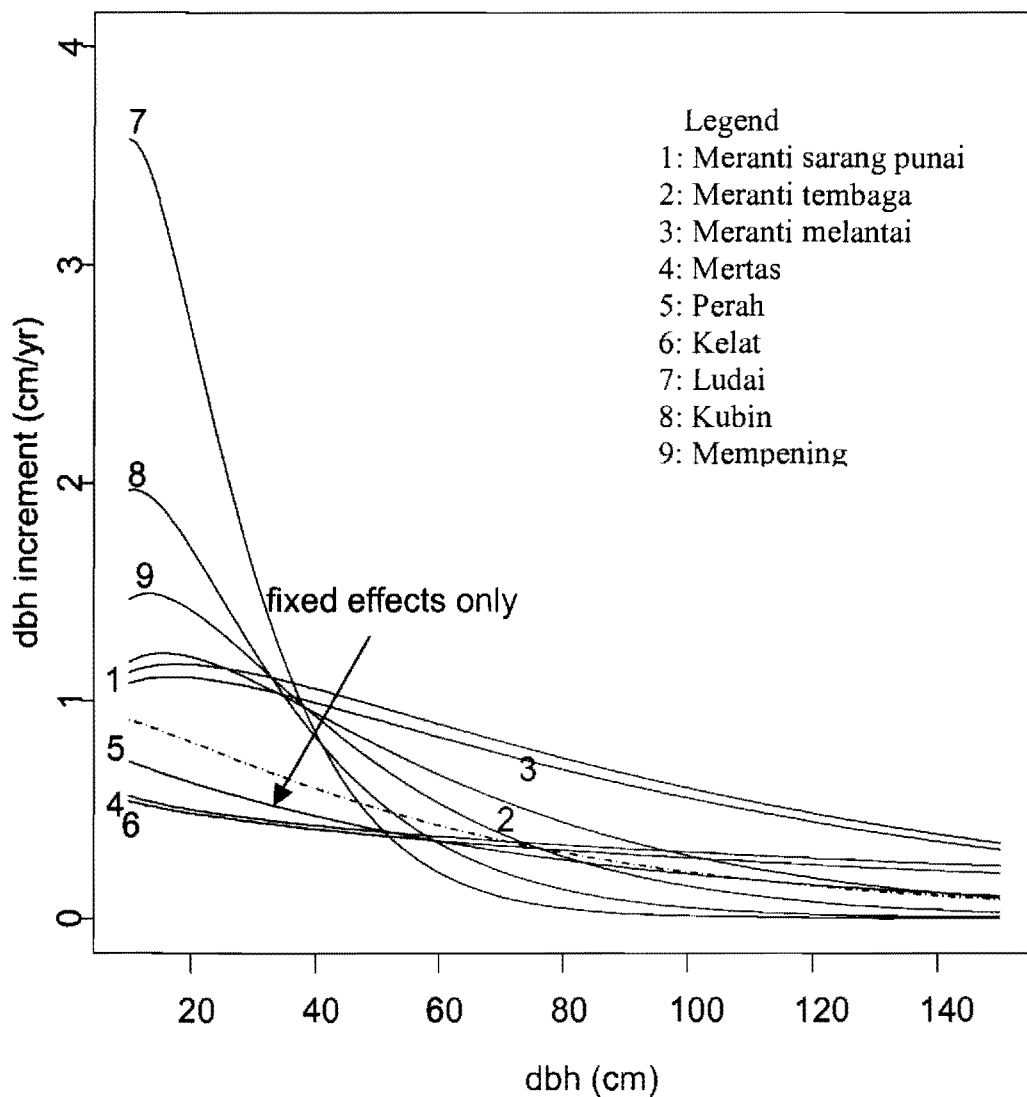


Figure 29: Predicting dbh increment versus the range of dmax using the non-linear random coefficients model [21] when dbh = 30 cm, osdi1.6=100 and sdi1.6=450. The growth curve with only fixed effect is also shown

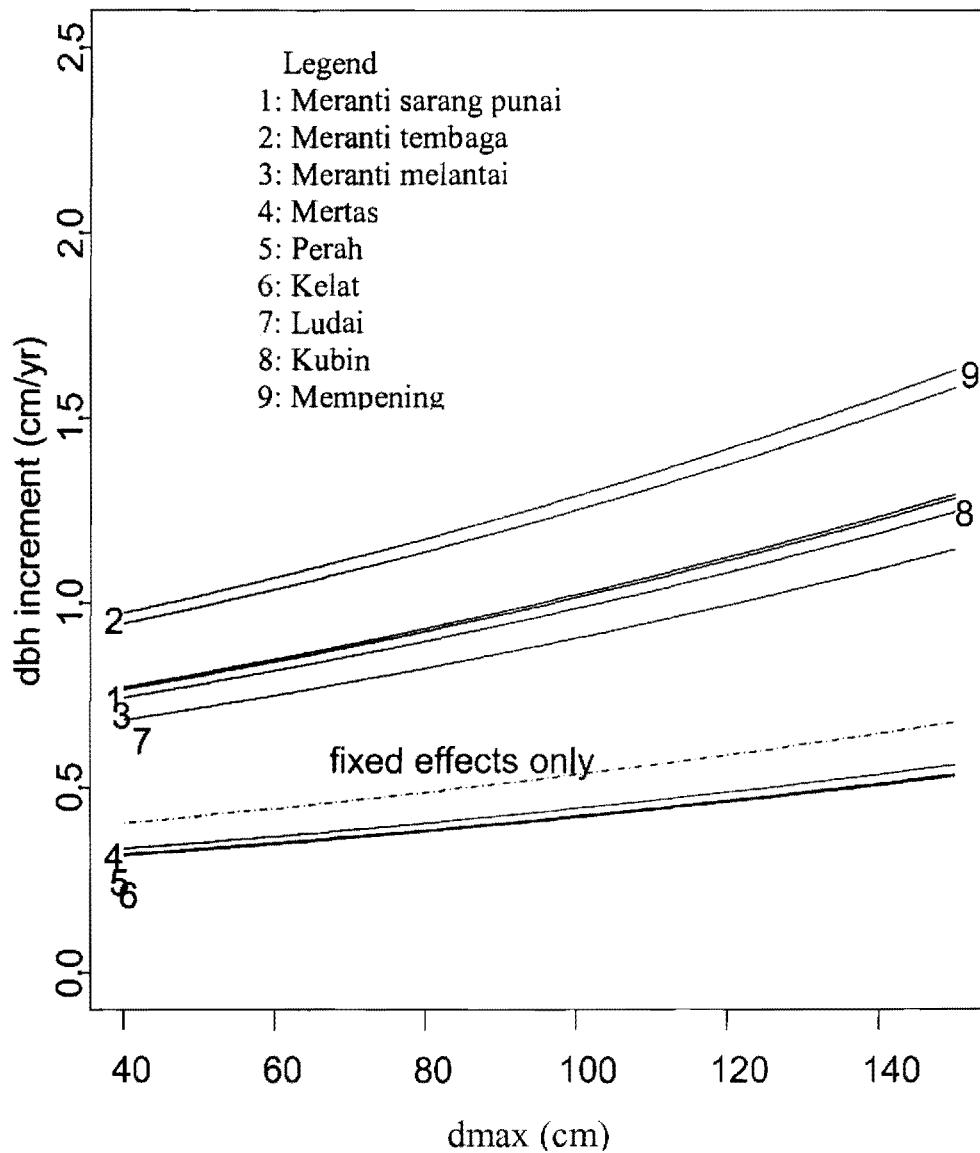


Figure 30: Predicting dbh increment over the range of tree dbh between 10<50 cm using non-linear random coefficients model [21] when $\text{osdi}1.6=100$, $\text{sdi}1.6 = 450$ and $\text{dmax}=60$. The growth curve with only fixed effect is also shown

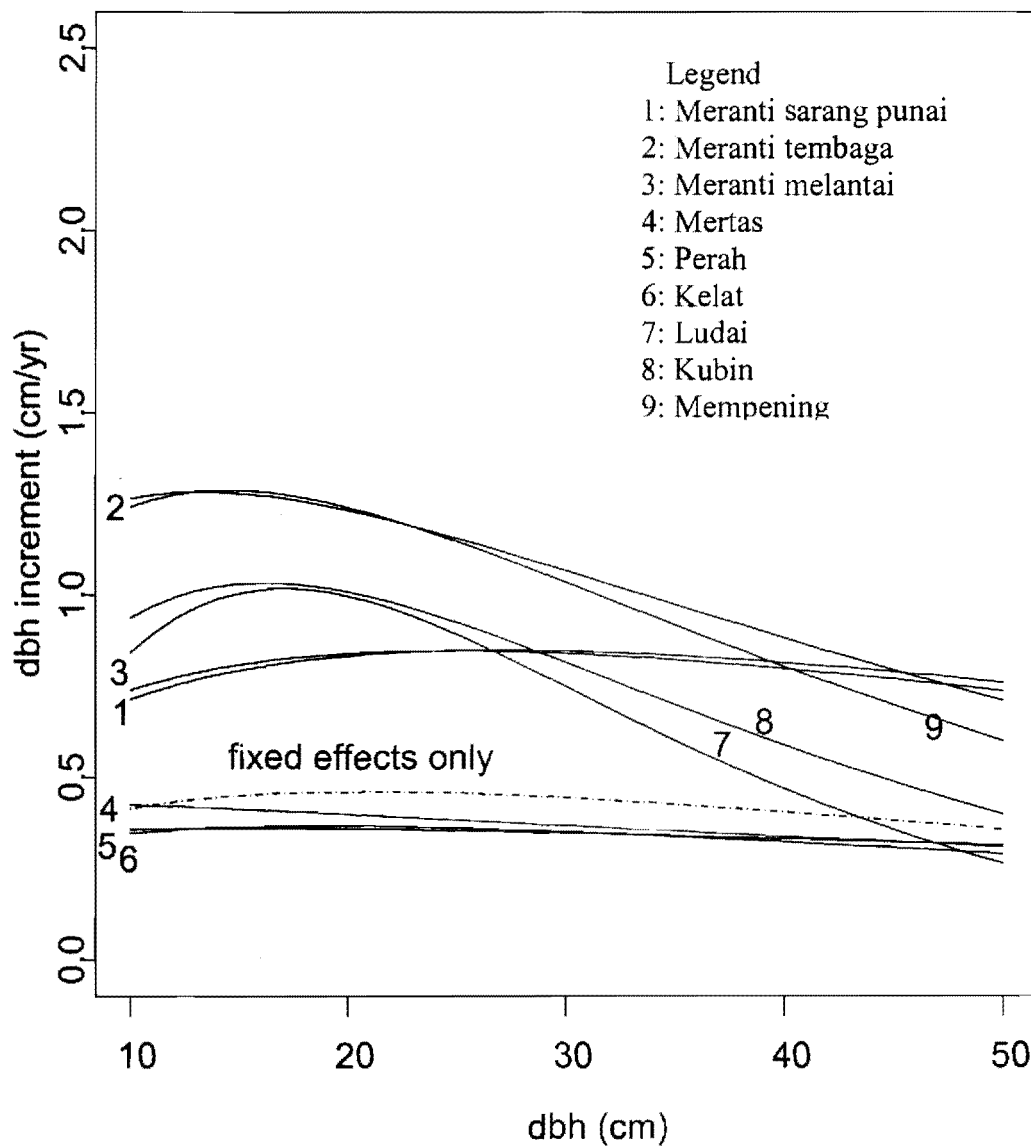
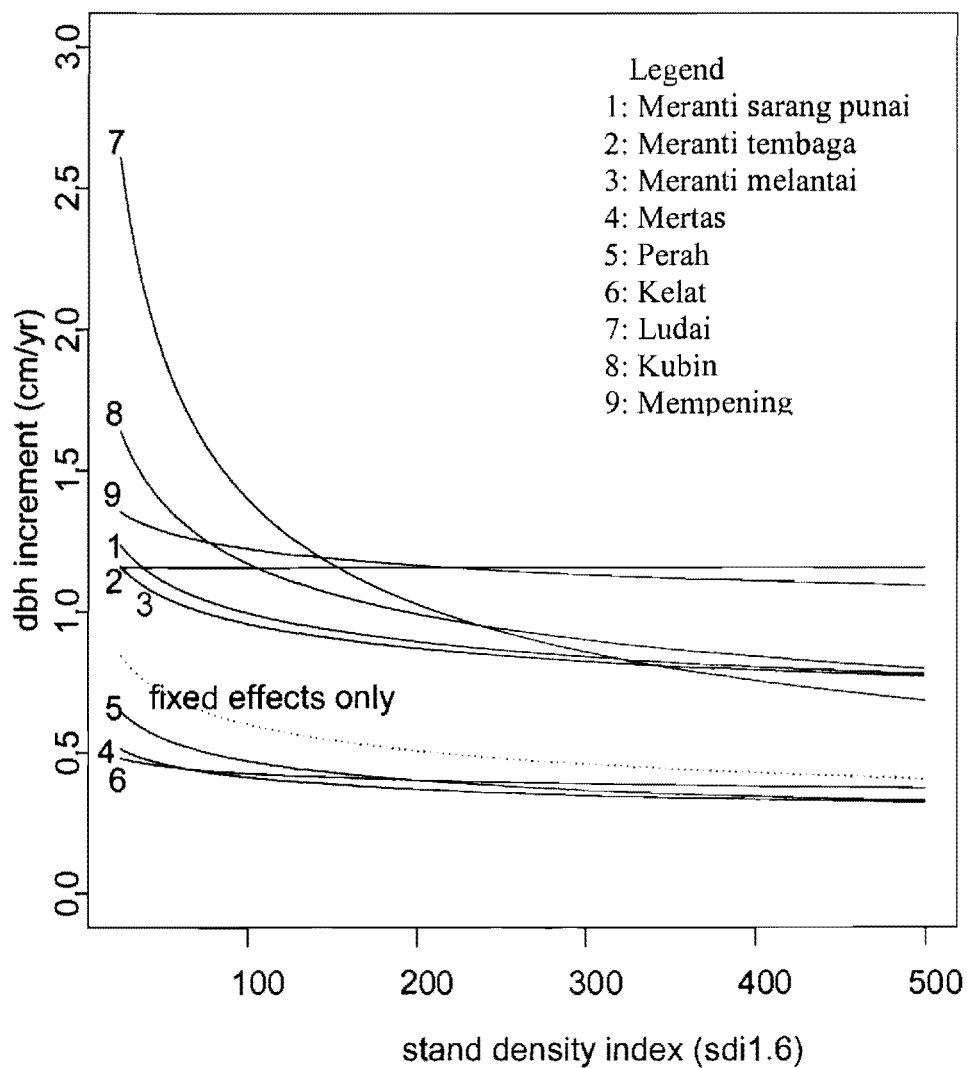


Figure 31: Predicting dbh increment due to competition from below using non-linear random coefficients model [20] when $dbh=25$, $osdi1.6=0$ and $dmax=25$. The growth curve with only fixed effect is also shown.



In general, the fluctuations in the growth pattern due to competition effects was obvious for the fast growing species. For the slow growing species, Kelat (*Syzigium sp*), Mertas (*Ctenolophon parvifolius*) and Perah (*Elateriospermum tapos*) their predicted dbh increment did not show any marked responses to competition effects.

It may desirable to have random species effects on parameters of all predictor variables, so that the effect of the predictor variables on the predicted response is specific to species. However, this approach would also run the danger of overparameterization. In the final model, four out of five predictor variables, i.e., dbh, $\ln(\text{dbh})$, sdi1.6 and osdi1.6, were permitted to be influenced by random species effects.

DISCUSSION

Biological Behavior of the Diameter Increment Model

The five predictor variables identified to influence the predicted dbh increment are the dbh, $\ln(\text{dbh})$, sdi1.6, osdi1.6 and dmax. The dbh coefficient is negative, and it determines the peak asymptote of the growth curve. The $\ln(\text{dbh})$ coefficient was positive and it allows a long right-hand tail of the increment curve, in turn allowing long-lived trees to attain large diameters. The sdi1.6 and osdi1.6 coefficients were negative indicating the negative effects of increasing tree competition and stand density on the predicted dbh increment. Lastly, dmax had a positive effect, indicating that increase in predicted dbh increment is associated with greater dmax under given stand condition as defined by sdi1.6 and osdi1.6. Higher dmax indicated that the range of tree size was larger or stand structure was more diverse than a stand with lower dmax, at a given sdi1.6. Hence, predicted dbh increment of trees in more structurally diverse stand was greater, and predicted dbh

increment also varied with the amount of $sd1.6$. The inclusion of random species effects on dbh and natural logarithm of dbh allows the growth curve to deviate from the population mean. Pioneer species grew fast in the early stage of growth development and reach the asymptotic peak much earlier than fast growing climax species. Variation in the coefficient of natural logarithm of dbh reflects the potential growth for larger size trees. The growth pattern described should be accepted with caution, because by changing the predictor variables in the model, the predicted dbh increment pattern might also change. In selection of the appropriate model, statistical significance should not be taken as the only criteria. Biologically rational signs on parameters are as important because they reflect logical consistency with the established behavior of tree growth. Bias may persist in some species, as depicted by the graph on boxplot of residuals by species (Figure 23a) but this situation is not so obvious when the non-linear model form was used (Figure 25). For obviously biased mean residuals within species, an alternative equation should probably be considered.

Relative Performance of Alternative Parameters on the Size-Density Limit

Three alternative slopes to the size-density limit were tested, i.e., 1.6, 2.0 and 2.6. The stand density index is derived by summation of individual trees within the plot. Slope equivalent to 1.6 gave the best fitted models based on the C_p statistics and adjusted R^2 value. The 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 slope of 2.6 was derived empirically from for mixed dipterocarp forest of Peninsular Malaysia (Chapter 2). The results from the analysis imply that variation in the diameter increment of trees in second growth forest can best explained by a lower value than that estimated size-density from primary mixed dipterocarp forest. In Chapter 2, the slope of 2.6 was derived from a long-term plot and the estimation was based on the geometric regression of $\ln(Dq)$ on $\ln(tph)$.

Sterba and Monserud (1993) have demonstrated that the maximum size-density limit of uneven-aged stands is influenced by the stand structural parameters, in turn implying that the limit changes for a given stand if its structure changes.

Linear vs Non-linear model

A linear model has been defined as a model that is linear in parameters, i.e., linear in the coefficients, while non linear models are nonlinear in their parameters. In the non-linear model, parameter estimates are not done by elementary matrix algebra, but by a more complex numerical algorithm that requires iteration (Raymond 1990). There are many techniques for fitting equations to data, and the appropriate one to choose depends on the nature of the data and the model. (Vanclay, 1995). The diameter increment equation was formulated to behave realistically across a wide range of stand conditions. The basic model that included only tree size variables was tested as both a linear model and intrinsically nonlinear model. The combination of initial tree DBH and its natural logarithm has the desirable property of allowing a peaking behaviour and asymptotically approaching zero for larger size trees. Analysis of the basic model indicated that a linear model is superior to a nonlinear model. In the mixed effects analysis, however, the nonlinear model was superior to the linear model, in part because the residuals plotted on covariates (DBH and the natural logarithm of DBH) indicated a more homogenous variance.

Species as Fixed vs Random Effect

Species diversity of the merchantable species is high in mixed dipterocarp forest. The regeneration sampling list of 1974 (Wyatt-Smith and Kochumen, 1999) reported that forty-three species were classified as preferred and fifty species as

acceptable. Modeling species has been difficult due to the usual inadequacy of sample size for a single species to develop a reliable estimate of the tree growth. In this analysis, species was treated as a random effect and all data were combined into one data set and analysed simultaneously.

Fundamental Behavior of Growth over Predictors

One of the main criteria in selection of predictors in a diameter increment model is 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 (osdi), stand density (sdi) and indicators of stand structure (dmax). The combined effect of initial tree dbh and its natural logarithm has the desirable property of allowing a peaking behaviour and asymptotic approach to zero as tree size increases toward a maximum. Increasing competition from above and increasing stand density have a negative influence on the diameter increment, as is universally observed in many forest types. Stand structure is represented in part by the maximum stand diameter (dmax), which implies that growth of a given tree is greater when dmax 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.

Levels of Species Aggregation

Trees were aggregated by vernacular names in this study. These names may represent a family, genus or species. Identifying species by vernacular names has advantages and disadvantages. The main advantage is that vernacular names are the level of species identification used in the operational forest inventory work; hence, the model can be applied to inventory data. The main disadvantage of

vernacular names to aggregate species is that, within certain groups specified by vernacular names, variation in silvical characteristics of the species can be very high. For example, Kelat (*Syzygium* spp.) is represented by 193 species and Medang (Lauraceae) by 180 species (Wyatt-Smith and Kochumen 1999). Most of the dipterocarps, especially the *Shorea* and *Dipterocarpus* were identified to species level. Although species identification was not done to the taxonomic species level, total vernacular names identified for the 18-one hectare plot still amounted to 207.

Species as a Predictor Variables (fixed effects)

The fixed effects models incorporate species effects. The mean residuals (Figure 20) fall closer to zero, relative to the models without any species effects (Figure 19). Although the fixed-effect models account for a species-effect, computations of species effects become prohibitive in nonlinear models. The number of parameters in the model increases directly with the number of species, and can add up rapidly if adding species effects on parameters for other covariates.

Differences in Model Assumptions Between Fixed Vs. Random Effects

Factor effects traditionally are either fixed or random depending on how levels of that factors are selected in a given study (Littell et al. 2000). A factor is considered fixed if the study represent specific levels of the factor that are of interest, rather than a random selection from many possible levels.. The effects of regression covariates are assumed to be fixed, i.e., in that the response is observed at specific levels of X. A factor is considered to be random if the levels of the factor represent only a random subset of a larger set of potential levels. The distribution of the population of random effects has mean zero and variance.

Differences in Estimation Algorithm Between Fixed Vs. Random Effects

The estimation algorithm for fixed-effects differs substantially from the algorithm for random effects. For example, the fixed effects model for a one-way classification is:

$$Y_{ij} = \beta_i + \varepsilon_{ij}, \quad i = 1, \dots, M, \quad j = 1, \dots, n_i$$

where the Y_{ij} is the diameter increment for tree j of species i , β_i represents the mean diameter increment of the i th of M species n_i trees are observed for species i , and the errors terms, ε_{ij} are assumed to be independently and identically distributed as $N(0, \sigma^2)$.

The random effects model for the one-way classification is:

$$Y_{ij} = \beta + b_i + \varepsilon_{ij}$$

where β is the mean diameter increment across the population of species being sampled, b_i is a random variable representing the deviation of the i th species from the population mean, and ε_{ij} is a random variable representing the deviation in diameter increment for observation j on species i from the mean diameter increment for species i . The error term for the within-species variability is denoted by $N(0, \sigma^2)$, and for the between-species variability by $N(0, \sigma_b^2)$.

Random Effect In Nonlinear Model Vs. Species-Specific Fits

A nonlinear mixed effects model was develop for the final model with species as random factor with effects on the intercept and slope of four covariates (dbh, log(dbh), osdi, sdi). In the final model, the coefficients for the intercept and these four covariates are assumed to be a random sample from some population of possible coefficients, and the regression model for each species is assumed to be a random deviation from some population of regression models. This type of analysis is sometimes called the random coefficient model (Little et al. 2000).

The fixed-effects term in the model described the average behavior of the entire population; thus the parameter estimates in linear fixed-effects and linear mixed-effects model were similar. Developing growth equations for every species has been a difficult task due to lack of sufficient data for reliable parameter estimation. In many cases species were grouped similarity in function (Vanclay, 1995; Ong and Kleine 1995). Mixed-effects model with random species effects makes it possible to develop growth equations for all species simultaneously in a single estimation algorithm. The random species effect allow the model to deviate from the population mean. Non-linear mixed-effects models allow the random species effect to enter in either a linear or non-linear manner, and in a simulation context varying levels of resolution with respect to species or species grouping can be accommodated by the same equation. The random effects on parameter estimates also allow the growth curve of individual species to deviate from the population mean, thus reflecting their unique growth behavior.

Application of the Models

The model developed in this analysis is suitable for predicting individual tree growth for mixed species forests. Although the data were obtained by

repeatedly measuring plots after initial logging, the time since logging was excluded as a predictor variable. Early exploratory analysis indicated that this was not a significant variable in growth estimation. Growth of individual trees was apparently responding primarily to tree-level and stand-level attributes, regardless of time since logging.

Grouping Species by Growth Behavior Summarized in Model Parameters

The nonlinear mixed effect model with a random species effect provides an opportunity for classification of species based on their growth behavior. As one example, cluster analysis of the species-specific parameter estimates for dbh and logarithm of dbh reveals distinct groupings of species at several levels (Figure 32). In this case a hierarchical clustering technique applying a divisive algorithm was used, but other techniques should be tested to verify the robustness of the groupings to clustering technique.

Figure 32: Cluster dendrogram of species in second growth forest based on the regression coefficient of DBH and natural logarithm of DBH



CONCLUSION

Several conclusions can be drawn from the study:

Random- and fixed-effects models produced similar parameter estimates for fixed predictor variables. Several drawbacks were apparent for the fixed-effects model. No estimates of the between species variability were provided, and the number of parameters to estimate is excessive in high diversity forests such as the hill dipterocarp forests of Peninsular Malaysia.

Mixed-effects models with random species effects made it possible to develop a growth equation for all species simultaneously in a single estimation algorithm. Addition of random species effects on parameters for predictor variables allowed the curves to deviate from the population mean, providing species-specific growth behavior.

Although little was gained in model fit between fixed and mixed-effects models, the error structure seemed to be better accommodated by the mixed effects model, as indicated by AIC and other diagnostics.

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APPENDICES

Calculation of Furnival Index for logarithmically transformed and non-linear model with derivative DINC

Unweighted linear regression

$$Y = \ln(\text{DINC} + 0.01)$$

$$dy/d\text{DINC} = 1/(\text{DINC} + 0.01)$$

$$\text{FI} = \text{rmse} * \exp[\ln(\text{DINC} + 0.01)]/n$$

Weighted non-linear regression (m=weight)

$$Z = (\text{DINC} + 0.01)/D^m$$

$$\begin{aligned} Dz/d\text{DINC} &= 1/D^{m/2} = D^{-m/2} \\ &= \text{GM}(dz/d\text{DINC})^{-1} \\ &= \exp[-m/2 * \sum \ln D/n]^{-1} \\ &= \exp[\sum \ln D/n]^{m/2} \end{aligned}$$

$$\text{FI} = \text{rmse} * \exp(\text{mean}(\ln(\text{DBH})))^{m/2}$$

Calculation of Furnival Index for logarithmically transformed and non-linear model with derivative of basal area growth (bag) with respect to DINC

The standard Furnival Index = $\text{rmse} * (f'(x))$

rmse is the residual mean square error and $f'(x)$ is the geometric mean of bag

Unweighted linear regression

Let $y = \ln[\text{bag} + 0.01]$

$$\begin{aligned} y = \text{bag} + 0.01 &= (\pi/4)(\text{DBH} + \text{DINC}) + (\pi/4)(\text{DBH}^2) + 0.01 \\ &= (\pi/4)(\text{DBH}^2 + \text{DINC}^2 + 2\text{DBHDINC} - \text{DBH}^2) + 0.01 \\ &= (\pi/4)(2\text{DBHDINC} + \text{DINC}^2) + 0.01 \end{aligned}$$

$$\begin{aligned} \text{dbag}/\text{DINC} &= (\pi/4)(2\text{DBH} + 2\text{DINC}) \\ &= (\pi/2)(\text{DBH} + \text{DINC}) \end{aligned}$$

Let $z = \ln(\text{bag} + 0.01)$

$$\begin{aligned} dz/d\text{DINC} &= (1/(\text{bag} + 0.01)) (d(\text{bag} + 0.01)/d\text{DINC}) \\ &= (\text{bag} + 0.01)^{-1} (\pi/4)(\text{DBH} + \text{DINC}) \end{aligned}$$

$$\begin{aligned} \text{GM}(dz/\text{DINC}) &= \exp(\Sigma \ln(dz/d\text{DINC})/n) \\ &= [\exp(\Sigma \ln(\text{bag} + 0.01) + (\Sigma \ln(\text{DBH} + \text{DINC})/n) + (\Sigma \ln(\pi/4)/n))] \\ &= \exp[\ln(\pi/4) - \ln(\text{bag} + 0.01) + \ln(\text{DBH} + \text{DINC})] \\ &= (\pi/4)(\text{GM}(\text{DBH} + \text{DINC})/\text{GM}(\text{bag} + 0.01)) \end{aligned}$$

$$\begin{aligned} \text{FI} &= \text{rmse} \cdot (\text{GM}[dz/d\text{DINC}])^{-1} \\ &= \text{rmse}(\pi/4)(\text{GM}(\text{bag} + 0.01)/\text{GM}(\text{DBH} + \text{DINC})) \end{aligned}$$

Weighted non-linear regression (m=weight)

$$Y = \text{bag} + 0.01/\text{bat}^{m/2}$$

$$\begin{aligned} Y = \text{bag} + 0.01/\text{bat}^{m/2} &= ((\pi/4)(\text{DBH} + \text{DINC}) + (\pi/4)(\text{DBH}^2) + 0.01)/\text{bat}^{m/2} \\ &= ((\pi/4)(\text{DBH}^2 + \text{DINC}^2 + 2\text{DBHDINC} - \text{DBH}^2) + 0.01)/\text{bat}^{m/2} \\ &= (\pi/4)(2*\text{DBHDINC} + \text{DINC}^2)/((\pi/4)(\text{DBH}^2)^{m/2}) \\ &= (\pi/4)^{1-m/2}(2*\text{DBHDINC} + \text{DINC}^2)\text{DBH}^{-m} \end{aligned}$$

$$dy/\text{DINC} = (\pi/4)^{1-m/2}(2\text{DBHDINC} + \text{DINC})\text{DBH}^{-m}$$

$$\ln(dy/\text{DINC}) = (1-m/2)\ln(\pi/4) + \ln(2) + \ln(\text{DBH} + \text{DINC}) - m\ln(\text{DBH})$$

$$\Sigma \ln(dy/\text{DINC})/n = (1-m/2)\ln(\pi/4) + \ln(2) + (\Sigma \ln(\text{DBH} + \text{DINC})/n) - (m\Sigma \ln(\text{DBH})/n)$$

$$\text{GM}(dy/d\text{DINC}) = \exp(\Sigma \ln(dy/\text{DINC})/n) = (\pi/4)^{1-m/2} 2\text{GM}(\text{DBH} + \text{DINC})(\text{GM}(\text{DBH})^{-m})$$

$$\begin{aligned}
 FI &= \text{rmse}[GM(dy/dDINC)]^{-1} \\
 &= \text{rmse}(\pi/4)^{(m/2)-1} 2[GM(DBH)]^m / GM(DBH+DINC)
 \end{aligned}$$

CHAPTER 4

APPLICATION OF THE MAXIMUM SIZE-DENSITY CONCEPT TO SILVICULTURAL PRACTICES IN HILL DIPTEROCARP FOREST: AN ASSESSMENT OF GROWING STOCK USING STAND DENSITY INDEX APPROACH

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APPLICATION OF THE MAXIMUM SIZE-DENSITY CONCEPT TO
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ABSTRACT

The maximum size-density concept has been fundamental to the practice of silviculture in temperate regions for several decades. This concept helps the silviculturist to design and implement strategies for achieving a wide range of stand structural objectives and desired species composition. Appropriate silvicultural strategies involving stand density manipulation require considerable insight into future stand development, especially the competitive effects depicted in stand density management diagrams at both the tree and stand level. In addition, stand growth and yield are intimately related to stand density regime. Density management can gainfully be implemented in a wide range of stand conditions, from even-aged to multi-aged structures. In the tropics the maximum size-density concept has been applied in managing teak plantations for timber; however, its applicability to natural tropical rainforest is still uncertain. Several lines of evidence from long-term plot data indicated the existence of a constant maximum size-density slope in dipterocarp forest. The implied maximum size-density limit and stand density index approach were applied to assess the growing stock before and after harvesting in productive hill dipterocarp forest of Peninsular Malaysia. Modification of the technique to improve its application to dipterocarp forests is briefly discussed.

Key words: stand density index, maximum size-density, growing stock, hill dipterocarp forest

INTRODUCTION

Silviculturists have applied the maximum size-density concept to managing timber stands in the temperate regions for several decades. This concept helps the silviculturist to design and implement strategies to achieve desired future stand conditions representing a wide range in stand structure and species composition. These strategies require accurate prediction of future stand development, including subsequent structure and competitive effects at both tree and stand levels (Jack and Long 1996). The silviculturist must also understand the basic concept of stand growth-growing stock relationships, as they are an important determinant of stand productivity and one that can be readily manipulated.

Predictive insights into stand development can benefit from various fundamental ecological concepts. Many quantitative tools applied in the practice of silviculture represents a blend of concepts from population ecology and forest biometrics. These tools help to assess and forecast various aspects of stand development. Design of effective silvicultural practices must consider the influence of density on stand structure, canopy dynamics and production efficiency (Jack and Long, 1996). Two related and widely known ecological concepts that have been applied in silviculture are the maximum size-density limit and the law of self-thinning. Reineke (1933) developed the concept of stand density index, by which a stand with any combination of mean dbh and trees per acre is standardized to a competitively equivalent number of 10-in (25.4 cm) trees. Specifically,

$$sdi = tpa (Dq/10)^{1.605}$$

where Dq is in inches, or its metric equivalent where Dq is in cm,

$$sdi = tph(Dq/25.4)^{1.605},$$

For stands of a fixed sdi

$$\ln(\text{tph}) = b_0 - 1.605 \ln(Dq), \text{ or } \ln(Dq) = b_0^* - 0.625 \ln(\text{tph})$$

In Reineke's (1933) analysis, different species were noted to have differing intercepts, but similar slopes.

Yoda et al. (1963) introduced a similar maximum size-density concept known as the $-3/2$ power law of self-thinning; however, they addressed pure even-aged stands of plants, they characterized the stands by number per unit area and average mass, and they looked at the movement of the stands over time with respect to logarithmic axes of these two attributes. Drew and Flewelling (1977,1979) introduced the $-3/2$ law of self-thinning into the forestry literature by relating number of trees per unit area to average stem volume. In recent decades this concept has been expanded in temperate regions to uneven-aged, single species stands (Long and Daniel 1990, Cochran 1992) and uneven-aged, mixed-species stands (Sterba and Monserud 1993).

In contrast the application of the maximum size-density concept in the tropics appears limited to a stand density management diagram for teak (*Tectona grandis*) plantations in India (Kumar et al. 1995). The applicability of this concept to more complex forest ecosystems is still uncertain, particularly in the tropics. Reasons for this uncertainty are:

- a) the concept was originally developed for pure or mixed even-aged stands in the temperate region (Drew and Flewelling 1977,1979);
- b) techniques and theory for applying the concept to more complex forest stands have emerged only in the last decade (Long and Daniel 1990; Puettman et al. 1992 ; Sterba and Monserud 1993);

- c) because the tropical rainforest is perceived as a very complex forest ecosystem, many foresters assume that they will demand more complex quantitative tools and management approaches;
- d) European classical silviculture, which was less quantitative than Japanese and American approaches, has had a strong influence in the tropics; and
- e) many external factors other than scientific principles, such as social and economic factors, influence silvicultural decisions in the tropics.

In tropical forest management, timber harvesting practices are considered or recommended first and foremost as a silvicultural treatment, provided damage to the residual stand can be minimized. The need to control logging damage in the tropics has led to the development of reduced impact logging technology. This development has now provided an important support tool for silviculturists to design and implement strategies that achieve desired management objective.

In principle, the productivity of managed forests can be improved through silvicultural practices, such as control of stand structure or developmental processes, control of species composition, control of stand density, restocking of unproductive areas, control of rotation length, facilitation of harvests and conservation of site productivity (Smith et al.1997). The first three silvicultural practices are very important determinants of stand productivity and can be manipulated directly by foresters, provided a quantitative assessment of the growing stock is available. Although quantitative guidelines have been developed for many temperate forests, the principles may apply to mixed dipterocarp forest of Peninsular Malaysia as well.

Various silvicultural practices have been adopted in Peninsular Malaysia and these can be broadly classified into systems based on origin of the next crop tree: natural regeneration simulated after harvest (e.g. Malayan Uniform System) or

intermediate size trees released by selectively harvesting large, mature trees (e.g. Selective Management System). Under the Malayan Uniform System, sufficient stocking of regeneration is a prerequisite of logging entry, which releases regeneration by removal of canopy trees and by subsequent girdling of non-commercial trees down to 15 cm dbh. Any intermediate size trees of commercial species were considered a bonus. The Selective Management System, however, relies on an adequate number of potential residuals for the next cut after 30 years. If potential crop trees or their equivalent are inadequate, the management may revert to the Malayan Uniform System on a 55-year cutting cycle (Thang 1997). Appanah et al. (1997) equated the system to high grading since it culls out the best commercial timbers; instead, they suggested a selection system to overcome this problem. Appanah et al. (1997) briefly laid out the steps required to implement the selection system by suggesting some modifications to the existing selective management system.

The objective of this paper was to develop an alternative procedure for assessing the growing stock of primary hill dipterocarp forest using a modification of stand density index as developed by Reineke (1933) for even-aged stands, and for designing silvicultural strategies to achieve the desired stand conditions. First, we review the concept of maximum-size density and its application to even-aged and uneven-aged stands. Second, we test the hypothesis that maximum size-density limit control stand trajectories in dipterocarp forests. Finally, we demonstrate the application of maximum stand density index to assessing growing stock of a hill dipterocarp stand. Our goal is to demonstrate the potential application and the flexibility of stand density index and maximum size-density limits to designing and implementing silvicultural strategies that will achieve desired future stand structures and species mixtures for productive hill dipterocarp forest.

MAXIMUM SIZE-DENSITY CONCEPT

Determination of Stocking Levels in Even-Aged Stand

Reineke (1933) developed the stand density index as an expression of stand density in even-aged conifer forests. He found that in pure, even-aged, fully stocked stands the number of trees per unit area were similar for stands with a given mean stand tree diameter. The maximum or average number of trees for a given diameter varied considerably between species but was generally consistent within species regardless of age and site quality.

The relationship between the number of trees and mean stand diameter of trees in fully- stocked stands was shown to conform to the following average relationship;

$$\ln N = -1.605 \ln Dq + k \quad [22]$$

where N is the number of trees per acre, Dq is the quadratic mean diameter and k is a constant varying by species. When k is 4.605 the curve passes through the point representing Dq=10 inches (25.4 cm), and N=1000 trees per acre (2500 trees per hectare).

Long (1985) stated that the advantage of Reineke's sdi is the ease with which it can be estimated and applied. The SDI for a stand is the number trees per ha (tph) that exerts an equivalent degree of inter-tree competition as the observed Dq and N in the subject stand. Given the observed tph and Dq, sdi can be calculated with the formula;

$$sdi = tph (Dq/25.4)^{1.6} \quad [23]$$

where Dq is in cm

Given any two of the stand parameters tph, Dq and sdi, it is possible to solve for the third following simple algebraic manipulation:

$$\text{tph} = \text{sdi} (\text{Dq}/25.4)^{-1.6} \quad [24]$$

$$\text{Dq} = 25.4 (\text{sdi}/\text{tph})^{0.625} \quad [25]$$

sdi has been used to assess and control the level of growing stock in forest stands. The manipulation of growing stock, and ultimately stand structure, can accomplish numerous management objectives; for example, sdi can be related to ungulate hiding and thermal cover (Smith and Long 1987), northern goshawk nesting habitat (Lilieholm et al. 1994), Mexican spotted owl habitat (Fieldler and Cully 1995), susceptibility to mountain pine beetle attack (Anhold et al. 1996), and amount and average size of timber (Kumar et al. 1995).

Application to Uneven-Aged Stands

Sdi is a simple function of Dq and trees per hectare as indicated in equation [2]. An alternative way to calculate sdi is by summation (Long and Daniel 1990; Cochran 1992) because the relative densities of individual stand components can be considered additive (Stage 1968). Long and Daniel (1990) therefore suggested the following general expression of sdi, extendable to uneven-aged stands:

$$\text{sdi} = \sum \text{tph}_i (\text{D}_i/25.4)^{1.605} \quad [26]$$

where D_i is the diameter (in cm) of the i th tree or diameter class in the stand and tph_i is the number of trees per hectare represented by the tree or diameter class i . For even-aged stands with a normal distribution of diameters, the two methods of calculating sdi (model [22] and model [26]) are equivalent. However, for a stand in which the diameter distribution varies from normal, the two estimates of sdi tend to

differ (Long 1990; Long 1996). Zeide (19) notes that the two approaches are equivalent if a “Reineke mean diameter (D_R)” replaces quadratic mean diameter.

$$D_R = (\sum sdi^{1.6} / n)^{1/1.6}$$

The summation is more desirable for the two following reasons (Long and Daniel 1990):

- a) the equation for even-aged stands is not appropriate for the skewed diameter distributions which are typical of uneven-aged stands, and
- b) it is not just the total sdi that is important in uneven-aged stands, but also the way this growing stock is partitioned among the various size classes.

Numerous authors have recently described the advantages of sdi allocation over traditional methods such as the B-D-q approach to regulating uneven-aged stands (Long and Daniel 1990, Cochran 1992, Long 1996, and Long 1998). The sdi method for controlling stocking in two-storied stands has also been advocated by Long (1996) particularly when competition is two-sided. In general, stand density index is a robust and practical way to assess and regulate growing stock across a wide range of stand structures, from even-aged to multi-aged stands including very irregular stands (Long 1998).

THE PENINSULAR MALAYSIA CONTEXT

Assessment of Residual Growing Stock under the Selective Management System

The Selective Management System (SMS) is currently practiced in all productive forest estates in Peninsular Malaysia. According to Shahrudin (1997), SMS was specifically designed for managing the hill dipterocarp forest. The system

allows determination of the appropriate cutting regimes based on a pre-felling inventory that assess three basic conditions: 1) the need to leave behind sufficient stocking of intermediate-sized trees, 2) economic viability of the cut, and 3) maintenance of initial species composition in the residual stand. Post-felling inventories are conducted to assess the adequacy of residual stocking.

In SMS, the assessment of the residual growing stock is based on “minimum residual stocking standards”. The minimum residual stocking of medium size trees (dbh class 30 – 45 cm) should not be less than 32 sound well-formed, marketable trees per hectare, or its equivalent in other size classes (Thang 1987, 1997; Shahrudin 1997). Tree equivalent refers to the convention that one tree with dbh greater than 45 cm dbh is equivalent to two trees with dbh between 30 and 45 cm dbh, while three trees of 15 – 30 cm dbh are equivalent to one with 30 – 45 cm dbh (Table 31).

Table 31: Minimum residual stocking standards under SMS

Class	Size	Number of trees per ha at next cut	Trees(s) equivalent to no. of trees in the 30-45 cm dbh class
Exploitable	+45 cm dbh	25	2
Ingrowth	30 – 45 cm dbh	32	1
Small trees	15 – 30 cm dbh	96	(1/3) trees below 30 cm dbh are not generally considered for the next cut)

Sources (Thang, 1997)

Some Evidence for the Existence of a Maximum Size-Density Limit in Dipterocarp Forest.

Knowledge of maximum sdi is essential for effective application of the density index approach. Maximum sdi is typically based on the sdi of stands that are assumed to be at their maximum size-density limit as described by equation [1]. The maximum size-density relationship in lowland and hill dipterocarp forest of Peninsular Malaysia has been examined with long-term ecological plots (Chapter 2).

Our preliminary findings for primary hill dipterocarp forests indicated that the maximum size-density slope is quite consistent (Figure 33). The two stand trajectories deviated from the average slope for short periods, but return to the same size-density limit after a few years. The departure of the stands from the maximum size-density line and their eventual return reflected natural disturbance and subsequent tree recruitment, residual growth, and resumption of density-dependent mortality. The regression slope of the logarithm of quadratic mean diameter on the logarithm of trees per hectare using the geometric mean regression technique (Ricker 1984), based on growth periods with only density-dependent mortality, was estimated to be -2.61 .

When plots representing logged mixed hill dipterocarp forest are plotted on a stand density diagram, the size-density trajectories are below the maximum size-density limit of the primary hill dipterocarp forest (Figure 34). Another approach would be to develop a maximum size-density in which the slope and intercept of the limit varied by stand structure and/or species mix (Sterba and Monserud 1993). Although, this approach could provide a reasonable assessment of current relative density, it would imply a moving target. For silvicultural field assessment a reasonable working hypothesis is that primary hill dipterocarp forest is close to the desired stand structure and species composition of managed hill dipterocarp.

Figure 33: Maximum size-density trajectory in Bukit Lagong Forest Resrve (hill dipterocarp forest) and Sungei Menyala (lowland dipterocarp forest) from repeated measurements between the period 1947 to 1997

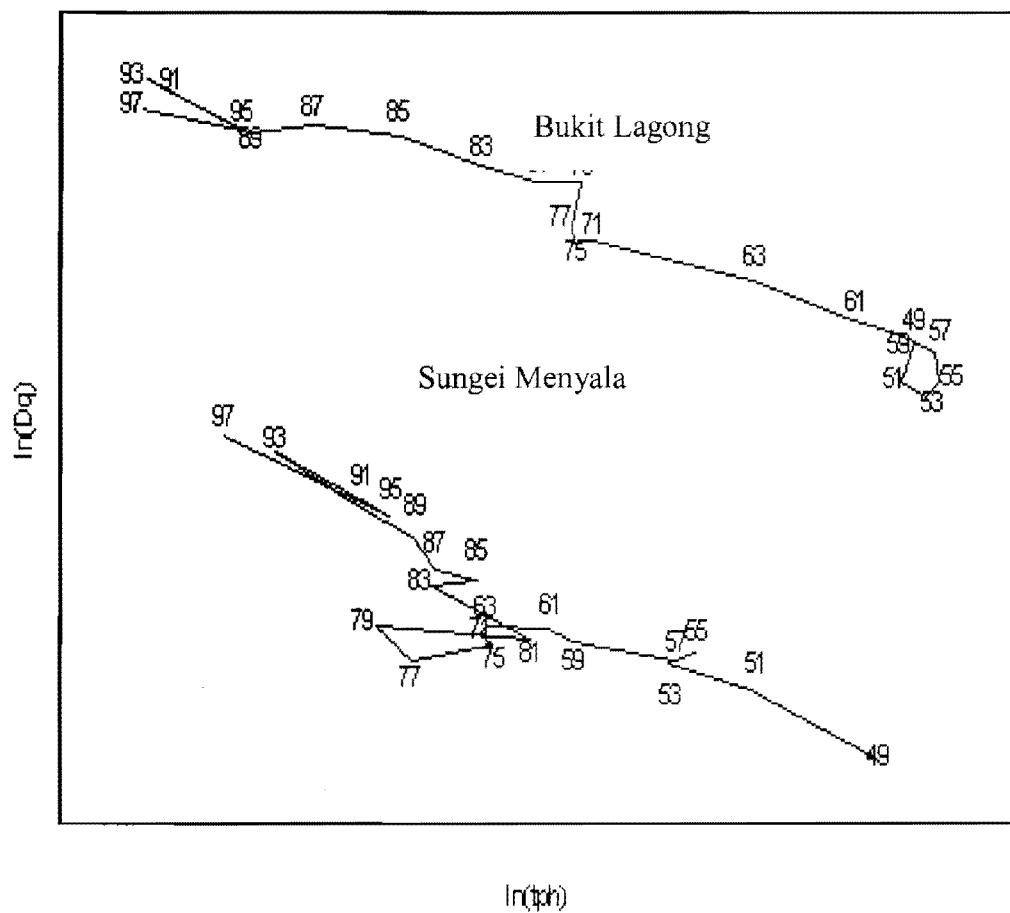
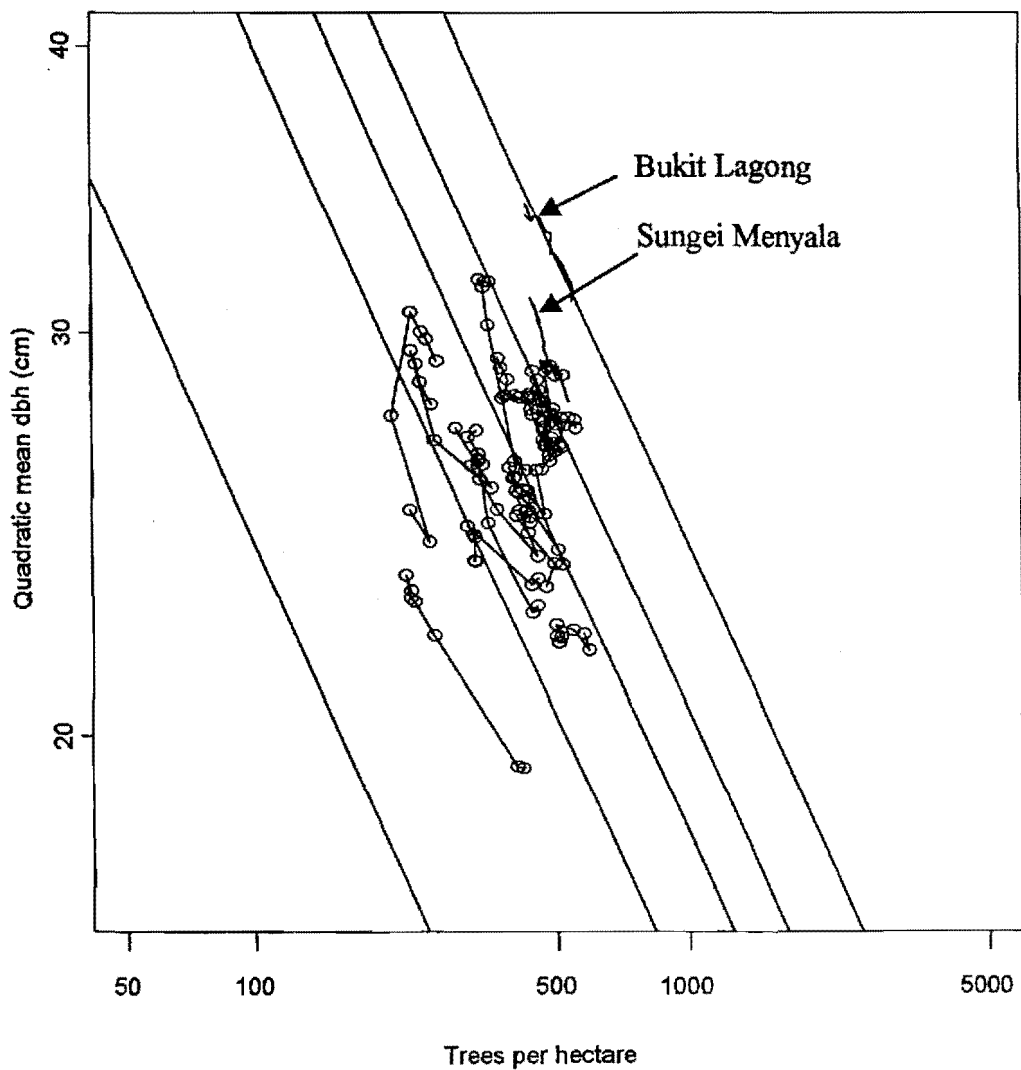


Figure 34: Size-density trajectory of 18 one-hectare logged hill dipterocarp forest in Tekam Forest Reserve based on the successive measurements between immediately to fifteen years after logging. The parallel lines indicate the relative stand density index. The maximum size-density trajectory of Bukit Lagong and Sungei Menyala Forest Reserve are also shown.



JUSTIFICATION FOR STAND DENSITY INDEX APPROACH

The concept of maximum density limit and allocation of growing stock to different size classes in uneven-aged temperate forests is relevant to the management of uneven-aged and mixed species stands of dipterocarp forest. Most primary dipterocarp forest are diverse in size-structure and species mixture. Thus applying sdi approach to silvicultural practices in dipterocarp forests offers several advantages :

- a) The sdi approach considers maximum growing capacity of the stand. Allocation of growing stock can be made based on the implied growing space occupied by trees of different size and species.
- b) The combined allocation of growing stock to size classes and species provides many options for the silviculturist to design a stand that would meet management objectives. It provides flexibility for meeting a variety of management objectives, for example, creating structures with a higher allocation of growing stock among intermediate size classes that can contribute to the next cut.
- c) The silviculturist can provide more options to aid managers in making decisions that will meet the desired management objectives.
- d) The method has been successfully applied to uneven-aged stands in temperate forests.
- e) The sdi approach allows for application of both selection and/or selecting cutting system as described later in the example. In the selection process, trees of poor quality will be removed, thus leaving a better quality stand after treatment. In the present Selective

Management System, a prescribed cutting limit is determined based on a pre-felling inventory. Selective cutting of large trees greatly reduced the size structural diversity of the stand. Phenotypically superior trees will be removed from the stand, leaving behind a poor quality stand.

- f) Mixed dipterocarp forest after selective logging is more diverse in stand structure and species mixture. The number of large size timber trees will be less as compared to the primary forest. The quality of the stand would be poorer, since most of the fast growing commercial timber trees have been removed from the stand. Application of the selective cutting method such as the SMS, might not suffice to create enough growing space for residual trees because fewer trees above prescribed minimum cutting limits will be removed from the stand.
- g) Assessment of growing stock based on sdi helps the silviculturist to determine the density of the second growth stand relative to the potential or maximum growing capacity of the managed forest. In some regenerated forest, the carrying capacity has reached the maximum level equivalent to primary dipterocarp forest (Manokaran 1998). The total sdi of the stand would indicate the status of growing capacity of the stand and the need to create more growing space for residual growth through silvicultural intervention.
- h) The approach is based on simple quantification of stand measures such as mean size (e.g. quadratic mean diameter) and density (e.g. trees per hectare) which can be easily understood by foresters.

Despite many advantages of the sdi approach in relation to the current management system of dipterocarp forest, there are still some shortcomings that need further investigations before it can be implemented in mixed dipterocarp forest.

- a) There is a limit to improving the quality of the growing stock through manipulation of stand structure and species mixture. For example, under present management, the assessment of species composition is based on two major species groups, Dipterocarps and Non-Dipterocarps, and in many forest the composition of Dipterocarps is as low as 10 % of the total density. In very poorly stocked areas, other options such as silvicultural intervention through planting of fast growing timber trees may be necessary.
- b) sdi approach alone generally does not include a component on regeneration. Research needs to be intensified on the regeneration responses to different levels of over-storey growing stock.
- c) There is still largely a lack of information on the growing space occupancy by species or species groups. The maximum size-density slope for the sdi calculation may vary between functional groups of species, i.e., the area occupied by the species at a given stand density. The shade-tolerant species usually occupy higher growing space than shade tolerant species for a similar stand density.
- d) The sdi approach assumes that mortality occurs due to competition or density dependent mortality. This basis is not well established in mixed dipterocarp forest, where a stand may consist of trees with different functional group, e.g., shade-tolerant vs. shade-intolerant, or they may occupy different strata, e.g., understorey, main canopy,

emergents and pioneer species. Many trees are affected by the competition for light.

Several problems associated with SMS approach are highlighted:

- a) tendency for culling, creaming or high-grading of the phenotypically superior species.
- b) consideration for selection of the cutting limits are only restricted to two major group of species, dipterocarps and non-dipterocarps only.
- c) no selection of trees to be retained was actually done in the field. Therefore no assurance that the residual stocking consisted of better quality trees and stands.
- d) in areas where dipterocarps are gregariously distributed and form high stocking of merchantable-size trees such as the Seraya-Ridge forest, allowing selective cutting would create a large openings and caused extensive damage to the residual stand
- e) no preference was given to allocation of growing stock by any form of growing space index. The main interest is adequate tree density of 30-45 cm dbh and/or its equivalence.
- f) there is always a tendency of lowering the cutting limits to the minimum. Manokaran (1998) reported several prescribed cutting limits approved for 26 location in three states of Peninsular Malaysia. The report reflects a tendency to prescribed the lowest cutting limits (i.e. 45 cm dbh for non-dipterocarp and 50 cm for Dipterocarps) in 42 % of the locations.

SMS was design for the primary hill dipterocarp forest. Unfortunately, most of the primary dipterocarp forests have been logged. Future timber production is more confined to second growth forest. In the second growth forest, many of the commercial timber trees, especially dipterocarps, have been removed from the

forest, and the stand is being dominated by species of lesser commercial value, and the timber is relatively small. As many large trees of dipterocarps have been removed from the stand, the future supply of adequate regeneration of dipterocarps is uncertain. At the landscape level, the forest is more diverse due to past disturbance created by logging. An immediate and important task seems to be the classification of the diverse condition of second growth forests, before any silvicultural intervention can improve the quality of growing stock. The sdi approach offers a flexible and appropriate strategy to achieve the desired management objectives under a changing environment and under varying degrees of forest condition, thereby ensuring the sustainability of timber production while maintaining ecological functions of the forest.

EXAMPLE OF GROWING STOCK ASSESSMENT USING STAND DENSITY INDEX APPROACH

We next demonstrate the stand density index approach to assessing and designing residual stand structures after the first entry in hill dipterocarp forest.

Data Description

The example shown below is based on a 6-ha ecological plot in Semangkok Forest Reserve. The plot dimension is 200 m x 300 m. The forest type is Seraya-Ridge Forest, with predominance of Seraya (*Shorea curtisii*), which is distributed mainly on the ridges and upper slope. The assessment was based on all trees greater than 5 cm dbh.

Preliminary Procedure

The procedure to design residual stand stocking, size structures and species composition of managed hill dipterocarp forest requires five major steps:

1. Identify the maximum stand sdi
2. Set level of residual growing stock (residual sdi)
3. Allocate growing stock by size class and species group
4. Specify the target residual stand structure by number and species mixture of trees in each size class
5. Assess probable impact of the silvicultural prescription through simulation of expected stand dynamics

We demonstrate the first four steps of the stand density approach while highlighting the fifth step in the discussion about factors to be considered. The assessment and specification of residual growing stock should achieve the desired residual stand stocking, stand structure and species mixture. In this example, the targeted stand stocking, size structure and species mixture were:

1. Residual stand stocking: 33 percent of the maximum sdi
2. Equal total proportion of dipterocarps and non-dipterocarps before and after treatment
3. Size structure: Higher proportion of the residual especially in the intermediate size-class
4. Species mixture: Higher proportion of dipterocarp species in all size classes after treatment than before treatment

Detail on the assessment of growing stock before treatment and allocation of growing stock after treatment is summarized in Table 32. Steps followed during this assessment and allocation were:

1) Identify maximum stand sdi

Determine the maximum size-density line for a fully stocked stand of primary hill dipterocarp forest. We assumed the slope of the maximum line is 2.61, based on the geometric mean regression of $\ln(Dq)$ on $\ln(tph)$ from repeated measurements in Bukit Lagong plot.

Compare the potential maximum sdi of the forest type to the pre-felling inventory data as currently collected under the Selective Management System (if first time logging entry). In this example, we assumed that the maximum sdi of the site is equivalent to the potential maximum sdi of the forest type. However, in general it may be desirable to assume that the pre-felling inventory reflects the maximum sdi for the site, particularly if there is no evidence of recent, unusually high mortality.

2) Set level of residual growing stock

- a) If desired residual stocking is 33 % of the maximum growing stock, then 67 % will be removed from the stand.

$$\begin{aligned}
 \text{Total residual sdi} &= \text{proportion of residual} * \text{Total sdi} \\
 &= 0.33 * 1435.8 \\
 &= 497.5
 \end{aligned}$$

In this example, trees were grouped into nine diameter classes and species groups Dipterocarp (D) and Non-dipterocarp (ND) (see Table 33).

Table 32: Stand density index and trees per hectare by dbh class before treatment and the assigned proportion of size structure and species mixture. Note: D is dipterocarps ND is non-dipterocarps

Dbh class (cm)	Before treatment						Proportion of sdi in each dbh class toProportion of D in total sdi each dbh class			
	Trees per hectare			Stand density index			Before treatment	After treatment	Before treatment	After treatment
	All	D	ND	All	D	ND				
15-May	601	40.7	561	44	2.8	41.2	0.03	0.05	0.06	0.10
15-30	189	16.7	173	124	12.1	112	0.09	0.15	0.10	0.15
30-45	67.7	8	59.7	180	22	157.6	0.13	0.25	0.12	0.17
45-60	25.5	5.3	20.2	168	38.4	129.8	0.12	0.2	0.23	0.35
60-75	11.2	4.2	7	141	54.7	86.7	0.10	0.15	0.39	0.73
75-90	6.5	4.5	2	137	98	38.5	0.10	0.1	0.72	1.0
90-105	5	2.8	2.2	163	93.5	69.9	0.11	0.05	0.57	1.0
105-120	2.2	2.2	0	100	100	0	0.07	0.05	1.0	1.0
120++	4.3	3.3	1	379	263	116	0.26	0	0.69	1.0
Total	913	87.7	825	1436	684	751.6	1	1	-	-

Table 33: The amount of removed and residual growing stock by stand density index and trees per hectare for each dbh class after treatment. Note: D is dipterocarps ND is non-dipterocarps

Dbh class (cm)	Stand density index						Trees per hectare					
	Residual			Removal			Residual			Removal		
	All	D	ND	All	D	ND	All	D	ND	All	D	ND
5-15	23.7	2.4	21.3	20.3	0.4	19.9	323.9	32.4	291.5	277.4	8.3	269.2
15-30	71.1	10.7	60.4	53	1.4	51.6	108.3	16.3	92.1	80.8	0.4	80.4
30-45	118.5	20.1	98.3	61.1	1.8	59.2	44.7	7.6	37.1	23	0.4	22.6
45-60	94.8	33.2	61.6	73.5	5.2	68.2	14.4	5	9.3	11.1	0.3	10.8
60-75	71.1	51.9	19.2	70.3	2.8	67.5	5.6	4.1	1.5	5.6	0.1	5.5
75-90	47.4	47.4	0	89.1	50.6	38.5	2.3	2.3	0	4.2	2.2	2
90-105	23.7	23.7	0	139.7	69.8	69.9	0.7	0.7	0	4.3	2.1	2.2
105-120	23.7	23.7	0	76.4	76.4	0	0.5	0.5	0	1.7	1.7	0
120++	23.7	23.7	0	354.9	239	116	0.3	0.3	0	4.1	3.1	1
Total	497.5	236.7	260.8	938.3	447.5	490.8	500.6	69.1	431.5	412.2	18.6	393.7

3) Allocate growing stock by size class and species group

- a) Calculate the sdi for each tree,

$$sdi_i = (D_i/25.4)^{2.61}$$

where i is the subject tree

- b) Classify the tree size according to tree dbh class and sum the tree sdi for each dbh class. In this example, trees were classified to 5-15 cm, 15-30 cm, 30-45 cm, 45-60 cm, 60-75 cm, 75-90 cm etc.

- c) Calculate the proportion of sdi in each class relative to the total sdi. For example, the proportion of sdi in size class 30-45 cm dbh will be

$$d) \text{ sdi for 30-45 cm dbh / Total sdi} = 0.13$$

- e) Calculate the proportion of sdi represented by species group in each dbh class. For example, the proportion of D sdi in size class 30-45 cm dbh will be:

$$\begin{aligned} \text{sdi for D / total size class sdi} &= 22.0/179.5 \\ &= 0.12 \end{aligned}$$

4) Design the desired residual stand structure

The target residual structure is designed by assigning a proportion of sdi to each size class. If the objective is to retain more residual growing stock in the intermediate size class after treatment, a higher proportion of growing stock should be assigned to these size classes. For example, if the proportion of the sdi of intermediate size class 30-45 should be greater after logging i.e. from 0.17 to 0.25, then the residual growing stock for that size class is,

$$\text{Total residual sdi} * 0.25 = 497.5 * 0.25 = 118.5$$

As shown in Table 32, the proportion of sdi assigned to the 30-45 and 15-30 cm classes increases substantially (Figure 35).

5) Design residual species mixture

Calculate the proportion of residual sdi allocated to each species group in each size class. If the composition of D should be greater after harvesting for size-class 30-45, then a higher proportion of D is allocated to that particular size-class. For example,

Proportion of D before cut = 0.12

Desired proportion of D after cut = 0.17

The targeted residual sdi for D at 30-45 cm dbh will be,

$$(\text{Proportion of D after cut}) * (\text{residual sdi}) = 0.17 * 118.5 = 20.1$$

The proportion of residual sdi allocated to D in each size class increases (Table 33, Figure 36).

In some cases, when the initial stocking of D in a certain size class is low, the targeted proportion of the D in the residual stand cannot be achieved. Hence, some adjustment may be required by increasing the proportion of D sdi in the adjacent upper or lower size class.

Figure 35: Proportion of sdi in each size class to total sdi before and after treatment

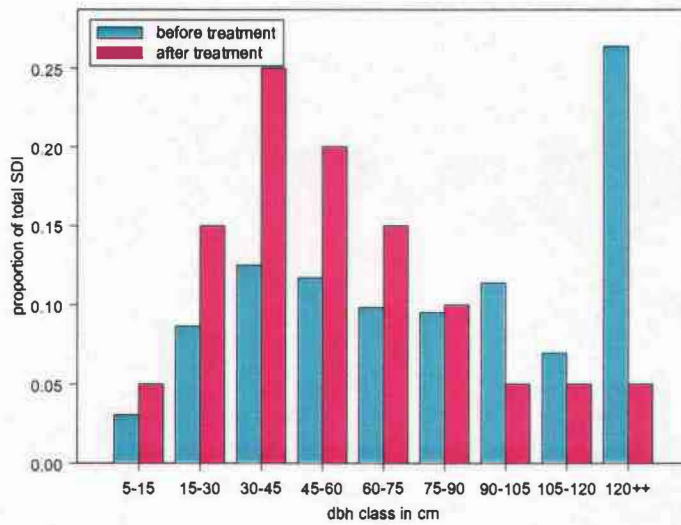
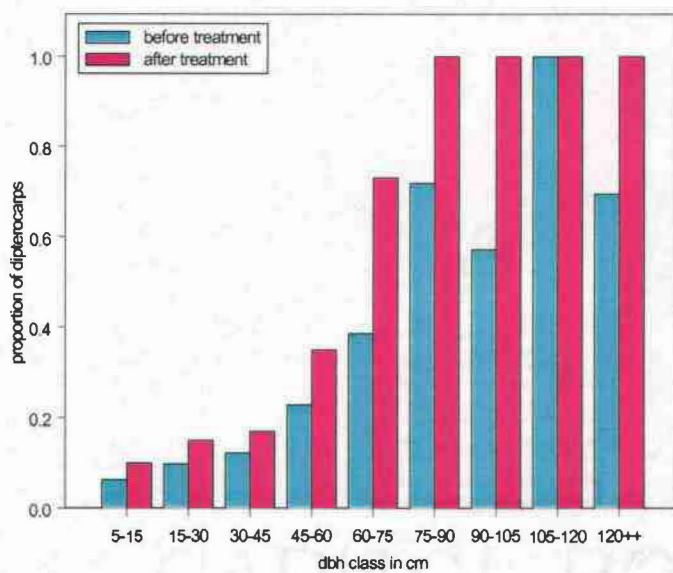


Figure 36: Proportion of dipterocarp sdi to total sdi in each size class before and after treatment



The proposed procedure for specifying stand stocking, size structure and species composition reflects a selection cutting for all size classes. Special considerations were given to maintaining an equal total proportion of dipterocarp sdi before and after treatment. A greater proportion of the growing stock was allocated to the intermediate size trees which will form the future timber production in the next cut. All non-dipterocarps greater than 75 cm were removed from the stand, while dipterocarps above 75 cm were preserved to regenerate the stand with dipterocarps (Figure 37 & 38).

Figure 37: Stand density index by dbh class before and after treatment.

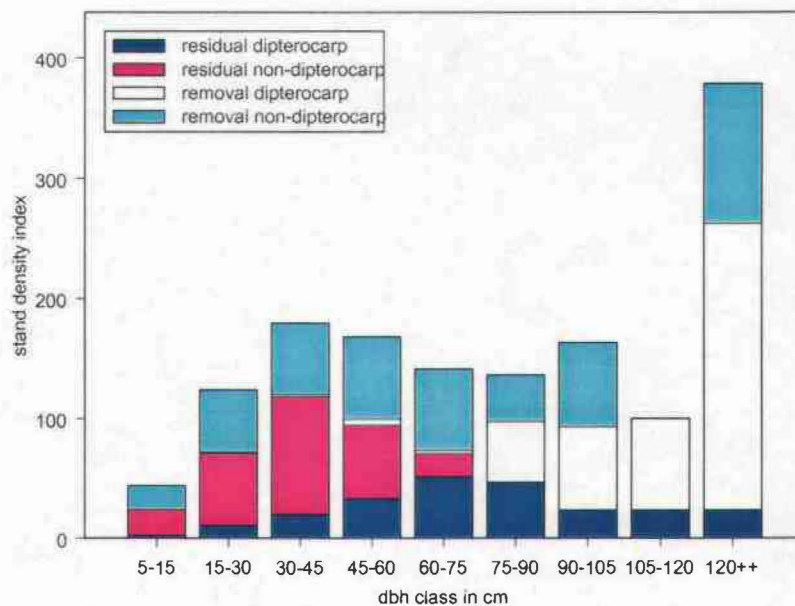
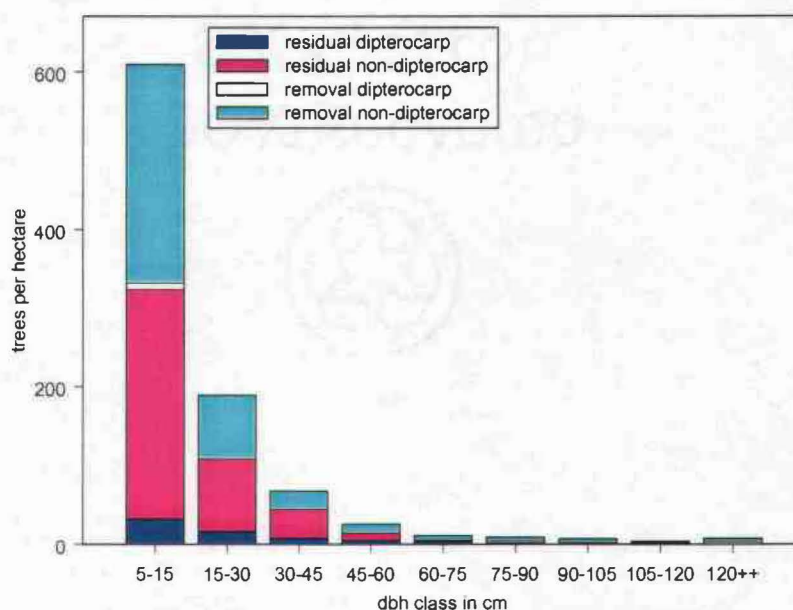


Figure 38: Trees per hectare by dbh class before and after treatment



FACTORS TO BE CONSIDERED

We have demonstrated a procedure of growing stock assessment and allocation for hill dipterocarp forest based on the maximum size-density concept. This concept however, is relatively new to tropical forestry. Several important factors should be considered in implementing this approach to mixed hill dipterocarp forest.

a) Maximum sdi for hill dipterocarp forest

The maximum sdi and maximum size-density slope for hill dipterocarp forest should be known before adopting this approach for assessing growing stock. Results from two long-term ecological plots monitored for almost fifty years indicated a trajectory with a size-density slope of -2.61, but the intercept values differ. In contrastst Manokaran and Swaine

(1994) indicated an approximately constant basal area from similar sites, implying that the slope of the maximum line is equal to 2.0. Other research (see Sterba and Monserud 1993) has shown that the slope is affected by stand structure and species mixture. Further research is required to determine how the maximum size-density slope varies by stand structure in hill dipterocarp forest. Then choice of an appropriate slope for current stand structure must be weighed against the slope of the target stand structure.

b) Management objectives

The desired stand structure and species composition depend entirely on management objectives. The stand density index technique offers a flexible approach to regulating stand density and structure and can therefore serve as a tool to attain specific silvicultural objectives. This tool has been applied in North America to meet wildlife, forest health and timber objectives (see Smith and Long 1987; Long and Daniel 1990; Lilieholm et al. 1994; Fieldler and Cully 1995; Anhold et al. 1996).

c) Total residual growing stocking retention

Total sdi reflects the degree of crowding between trees within the stand. Removal of a certain proportion of growing stock releases the residual trees for growth. Too much opening will often encourage the establishment of pioneers and may alter the future species mixture to include more undesirable species, unless the seedlings of commercial species are already present in abundance. The level of growing stock that will ensure optimal growth and composition of the residual stand needs to be investigated.

d) Calculating the sdi for a given species or species group

The hill dipterocarp forest species can be categorized into several functional groups. The most common classification distinguishes among emergent, main canopy and understorey species. These groups can be further sub-divided into shade-tolerant and shade-intolerant species. Other classifications have species distinguished by light demand, such as pioneer versus late-seral species. Each functional grouping would probably have different maxima for stand density index. Further research will be necessary to determine the sdi for each species or species group.

e) Quality and quantity of residual tree

Trees for retention are the potential crop trees and they comprise the bulk of the residual sdi. The potential crop trees should be free from climbers, and should be healthy, vigorous trees that would grow into the final crop trees. Specific criteria for identification of these trees need to be established; tree health, tree vigor, present of diseases, bole form, crown size, crown ratio, and species of interest. The selected species should also have high probability of living until the next crop cutting cycle. By actively selecting trees to be retained, the chances of retaining genetically inferior trees would be minimised, thus enhancing the quality and quantity of the stands.

f) Site productivity

Logging causes considerable damage to the soil by road construction and skid trail disturbance. The most fertile layer of the soil is excavated

for establishment of forest roads. High compaction, resulting low infiltration and high erosion rates, leads to long-term degradation of the forest soil. The productivity of the site with respect to forest growth can therefore decrease after logging. The potential maximum sdi for the site may be reduced as well, at least in the short term.

g) Logging damage to residual stand

Damage to the residual depends on the type of harvesting and the amount of growing stock removal, as well as topography of the forest stand. Greater removal has often been associated with greater damage to residual trees, and steeper slopes likewise can cause greater damage to both the residual trees and the ground surface. Damaged residuals should be removed from the stand, and therefore the amount to be retained should take potential damage into account.

h) Stand improvement through timber harvesting

In hill dipterocarp forest, removal of trees through harvesting has been regarded as the first major silvicultural operation. Due to silvicultural intervention, the residual stand should be of better quality than the original stand. Poorly formed trees, over-mature trees and trees which do not grow to harvestable size should be the priority for removal. Whitmore (1984) reported many Sapotaceae and *Calophyllum* spp. do not reach harvestable size. Manokaran and Swaine (1994) reported about 45 % of the species and 36% of the total number of trees > 10 cm dbh in the Bukit Lagong plot are understorey, pioneer or late-seral species which rarely reach the main canopy.

i) Retaining parent trees for regeneration

Parent trees are trees retained as a source for regeneration of the desired timber species. Total sdi represented by the parent trees should be considered in the allocation of residual growing stock. Under present management, one parent tree per hectare must be left behind.

j) Upper limit of growing stock for managed hill dipterocarp forest

The maximum sdi of the primary (undisturbed) hill dipterocarp forest indicates the potential carrying capacity of this forest type. In managed forests, the upper limit of management or the optimal stocking standards will be less than the maximum. Further research is required to address this issue. Cochran (1992) set an upper limit of 66 percent of the maximum sdi for managed uneven-aged ponderosa pine stands, yet Drew and Flewelling (1977,1979) define 55 % as the zone of imminent mortality. The existence and relative density of these zones remains to be investigated in managed hill dipterocarp forest.

k) Cutting cycle

Cochran (1992) suggested applying stand projection techniques to estimate the length of time needed for the residual stand to grow back to the upper limit of managed stands, as mentioned in item (i). If the estimated length of time is not a reasonable cutting cycle, the silviculturist might wish to raise or lower the stocking level and again project the stand forward in time. This approach would give the silviculturist information to guide decision makers on the appropriate level of cutting, balanced among many other expected benefits of the forest.

1) Abundance of natural regeneration

In Peninsular Malaysia, mast fruiting occurs at intervals of 5-7 years. A large percentage of trees in the forest fruit profusely, and the floor may be imbedded with carpet of seedlings after seed germination. The rate of mortality, however is high among the seedlings, especially in the subsequent years if no over-head release is provided. When timing of harvest coincides with the event of mast fruiting, and abundant stocking of regeneration from the commercial timber species is present, the silviculturist might consider removing a high proportion of the over-storey trees to allow sufficient sunlight to reach the under-storey, while still maintaining the total targeted residual growing stock.

CONCLUSION

The background of stand density index and a maximum size-density approach to regulating growing stock has been described. Although the technique was developed in pure even-aged stands in the temperate region, it has recently been extended to uneven-aged and mixed-species forest. The technique provides a quantitative approach to obtaining the optimum yield through the manipulation of stand stocking, size structures and species mixtures. The technique, therefore, has potential application to managed hill dipterocarp forests of Peninsular Malaysia.

The proposed and demonstrated stand density index approach concerned only trees with dbh greater than 5 cm. The regeneration component is an important determinant of forest sustainability. Inventory of regeneration provides the basis for the silviculturist to examine the regenerative capacity of the forest, and to design treatments that would improve the growth of this regeneration. In theory,

reduced over-storey growing stock provides more growing space to the understorey vegetation (O'Hara 1998), thus improving its growth through increased rates of photosynthesis. This concept has been successfully applied under the Malayan Uniform System (Wyatt-Smith 1963), where heavy removal of overstorey trees and subsequent girdling of pole-size and larger trees helps in releasing the commercial, light-demanding, understorey seedlings and saplings.

The spatial distribution of trees to be harvested and retained is not dealt with in this paper. The proposed method concerns assessment of current growing stock and specification of residual growing stock under silvicultural manipulation, assuming that strictly low-impact harvesting can be carried out.

The proposed assessment of growing stock for hill dipterocarp forest is still new to many foresters in Malaysia and perhaps in the tropics. The method is based on several assumptions that will require more field data to verify. Collaboration with other forestry agencies is required to gather more data and to examine the maximum size-density relationship in remaining primary hill dipterocarp forests. Preliminary research results have supported the existence of a consistent maximum sdi for hill dipterocarp forests, thereby providing a tentative basis to assess the growing stock in uneven-aged stands. This working hypothesis can be refined as more experience accumulates with applying this approach operationally.

Using the proposed method, silviculturists will have more flexibility in designing and implementing strategies to achieve established stocking standards, target stand structure and desirable species composition in managed forests. Numerous additional factors can then be superimposed on this framework to improve the assessment of growing stock and optimize forest conditions.

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CHAPTER 5

SUMMARY

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This research has provided several insights into the growth dynamics of trees at the tree and stand level in mixed primary and second-growth hill dipterocarp forests in Peninsular Malaysia.

The maximum size-density limit of primary forests was assessed taking into account stand structural parameters and tree community type from temporary sample plots. Results from regression analysis indicated that temporary plots data did not provide sufficient evidence to conclude a maximum size-density limit of hill mixed dipterocarp forest, at least at the spatial scale investigated. Future studies on maximum size-density in primary hill dipterocarp forests should consider appropriate plot size to account for the variability in the mean size and stand density. Findings from two long-term permanent sample plots in primary mixed dipterocarp forest indicated that the maximum size-density limit is quite consistent. Several stand trajectories deviated from the limit for short periods, but returned to the same limit after a few years. The deviation of the stands from an apparent size-density limit and their eventual return to the limit reflected tree recruitment and residual growth following release of growing space after individual tree mortality.

A random-effects model for individual tree dbh increment was explored. The basic model was selected using the Furnival Index. Covariates were selected based on C_p statistics and adjusted- R^2 from all-subsets regression analysis. The selected covariates reflect the tree size, competition, and stand size variability. Fixed effects models and random effects models were tested and compared. Random species effects allow estimation of the mean and variance of each species relative to the population of all species. Species effects on tree size covariates allow the curve to deviate from the population mean, and to reflect the unique behavior of individual species. The mixed -model approach also enabled reliable estimation of species-specific parameters simultaneously. The correlation among

trees within a plot and among repeated observations within a single tree over time were not addressed in the analysis.

A stand density index approach, based on the maximum size-density concept, was applied to assess the growing stock before and after treatment in primary hill dipterocarp forest of Peninsular Malaysia. This approach provides the flexibility for silviculturists to design and implement strategies of density management to achieve desired future stand condition. This approach is a modification of growing stock assessment using stand density index from uneven-aged temperate forests. Since the maximum size-density concept is relatively new to mixed dipterocarp forest, several factors to be considered were highlighted.

The understanding of the maximum size-density concept, development of a quantitative growth model and application of density indices to assessing growing stock will provide support for exploring the impact of management options and silvicultural alternatives on managed hill dipterocarp forest.

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