Research article

Assessment of allometric models for leaf area index estimation of Tectona grandis

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Abstract: We developed allometric models for accurate estimation of Tectona grandis (teak) leaf area index (LAI), for different stem diameter-classes (D-classes). In this study, we harvested teak trees in the tropical dry region of India in the ten stem diameter classes and measured LAI, and developed regression models for the non-destructive estimation of LAI with the help of wood density (ρ), diameter at breast height (D) and plant height (H). Models used for the prediction of biomass of tree components were of the form, linear, logistic, Gompertz and Chapman. Among the four models, non-linear models were more efficient compared to the linear model. We observed more than 60% variability in the LAI, explained by non-linear regression models. The models including ρ and D had greater $R^2$ and lower standard error of estimate. Our study detected logistic models more appropriate for broad diameter range and Gompertz models for small D-classes. The regression models developed in our study can be applied separately for the ten D-classes, and this could minimize the error occurring during indirect estimation of teak LAI.

Keywords: Tectona grandis - Leaf area index - Allometric models - Wood density - D-classes - Tropical dry region.

INTRODUCTION

Exchange of mass and energy of resources through plant canopies is functionally related to leaf area index (LAI) (Law et al. 2001, Moser et al. 2007, Woodgate et al. 2015). In forest ecosystems, LAI is an essential variable which controls solar energy, carbon flux and water. Usually, LAI is defined as the total one-sided leaf tissue area per unit of ground surface area (Watson 1947). It is a dimensionless quantity and an important characteristic feature of the canopy of an ecosystem. It is the most important parameter for modeling forest ecosystem processes, such as canopy photosynthesis, respiration and evapotranspiration.

Mostly, the studies for LAI have been carried out in temperate forests (Dufrêne & Bréda 1995, Sellin 2000, Temesgen & Weiskittel 2006, Weiskittel & Maguire 2006, Urban et al. 2009), and very few for tropical ecosystems (Maass et al. 1995, Nascimento et al. 2007, Vyas et al. 2010). The quantification of LAI is unfortunately, very difficult, due to its spatial and temporal variability (Bréda 2003). LAI has been observed to be sensitive to site differences and tree density (Gspaltl & Sterba 2011). It can be determined by harvesting, litter trap methods, optical sensors and laser scanning (LiDAR). For indirect measurements, optical methods and LiDAR are commonly used, which are based on Beer-Lambert law. Optical measurements are generally performed with using canopy analysers, hemispherical photography, and remote sensing (Bréda 2003, Jonckheere et al. 2004, Zhang et al. 2005, Dovey & Toit 2006, Arias et al. 2007, Nascimento et al. 2007, Urban et al. 2009, Huang & Pretzsch 2010). LiDAR applies threshold-based separation of laser reflections from the canopy and from the ground (Hosoi & Omasa 2006, Béland et al. 2011, Stark et al. 2015, Lin & West 2016). However, due to some functional limitations, these indirect methods, fail to measure LAI accurately in tropics, where the vegetation is dense and multi-layered (Moser et al. 2007). Inaccuracy in measurements has also been...
observed with non-random leaf area distribution and shading caused by plant parts (e.g. branches, stems), other than leaves (Pokorný & Marek 2000, Huang & Pretzsch 2010).

In the direct estimation of LAI, leaf areas of total leaves of the canopy have to be summed and divided by the canopy projected area. However, this process is time-consuming and impossible for the whole stand. Therefore, generally a limited number of trees are sampled, allometric equations are parameterized, and used for the other trees in the stand (e.g. Ledermann & Neumann 2006, Hietz et al. 2010, Laubhann et al. 2010, Gspaltl & Sterba 2011). Across the environmental gradients, LAI estimated by direct methods have been observed to be more accurate compared to the indirect methods (optical measurements) (Khan et al. 2005). A significant underestimation of LAI by indirect methods compared to the direct methods have also been observed, when the estimates were cross-validated (Bréda 2003). Therefore, for the accurate non-destructive estimation of LAI, allometric models are needed.

In the tropical dry region, plants shed their leaves during the dry period, therefore, for non-destructive estimation of LAI, leaf litter is collected in litter traps plotted below the canopy during the dry period (Marshall & Waring 1986, Bréda 2003). By using specific leaf area (SLA), allometric equations relating littermass and DBH (diameter at breast height) have been developed for the estimation of LAI (Gower et al. 1999). Several studies have also developed allometric models for LAI estimation relating foliage biomass, littermass, DBH, and ground area covered by the canopy (Li et al. 2005, Pretzsch & Mette 2008, Vyas et al. 2010).

Since, LAI is utilized to understand community, ecosystem, and global processes, there is great demand of better temporal and spatial data sets of LAI (Cornwell 2015). For accurate estimation of LAI, multispecies/multi-site allometric equation could not be applied over a large area. In different stem diameter-classes (D-classes), there are architectural changes in trees, therefore, allometric models are required also for different D-classes, separately (Chaturvedi & Raghubanshi 2015a). Common allometric models for LAI estimation have foliage biomass or littermass as the estimator, however, foliage allometric equations are supposed to be affected by tree size, species and edaphic conditions (Law et al. 2001). Errors in the measurement of LAI by littermass have also been observed due to environmental effects on litter SLA, particularly those concerning canopy structure and soil conditions (Bouriaud et al. 2003). Therefore, to minimize the error in LAI estimate, we chose wood specific gravity or wood density (ρ) as an estimator in the allometric model for LAI estimation. ρ is linked to stem strength, stiffness and safety (i.e. measured as dry wood mass per green wood volume), and ranges from 0.1 to 1.5 g.cm⁻³ among tropical trees (Chave et al. 2009, Zanne et al. 2009, Bastin et al. 2015). It is often used as a proxy for understanding the size and functioning of the tropical tree species (Swenson & Enquist 2007, Chave et al. 2009, Reich 2014). In several studies ρ has been used for developing biomass allometric models (Chave et al. 2005, Chaturvedi et al. 2010, Chaturvedi et al. 2012a, Chaturvedi & Raghubanshi 2013, Chave et al. 2014, Chaturvedi & Raghubanshi 2015a, Chaturvedi et al. 2017a).

Teak (Tectona grandis L.f.) is the most important timber-yielding, deciduous plant of the tropical belt (Sousa et al. 2012). This broadleaved tree species is native to India, Myanmar (Burma), Thailand and Laos, but nowadays grows in the whole intertropical region. Worldwide, teak plantations cover approximately 6.0 mha area (Bhat & Ma Hwan 2004) in which around 94% area is in tropical Asia, with a major part in India (44%) and Indonesia (31%) (Pérez 2005). In India, about 29% of the total forest area is dominated by teak (FSI 1998). Mostly teak is naturally found in western and southern India (Champion & Seth 1968). Its northern limit is western Aravalli and eastward through central India. Teakwood is moderately hard, easily worked and extremely durable, therefore, it has a high demand for yachting, building and furniture industries (Troup 1921, Tewari 1992). Due to high market demands, the establishment of plantations of teak is continuously increasing in several tropical countries beyond its native origin (Pérez & Kanninen 2003). In this study, we measured LAI of teak in ten D-classes, occurring in the tropical dry region of India, by harvest method and developed regression models for the non-destructive estimation of LAI with the help of ρ, D and tree height (H). Further, we observed the strength of similarity between the actual harvested LAI and those estimated by the regression models.

MATERIALS AND METHODS

Study area

The study was executed in the Vindhyan highlands situated in Sonebhadra District of Uttar Pradesh, India (21° 29’–25° 11’ N and 78° 15’–84° 15’ E). The area experiences tropical monsoon climate with three seasons in a year, viz, summer (April–mid June), rainy (mid June–September) and winter (November–February). The

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months of March and October constitute transition periods, respectively between winter and summer, and between rainy and winter seasons. The maximum monthly temperature varies from 20 °C in January to 46 °C in June, and the mean minimum monthly temperature reaches 12 °C in January and 31 °C in May. According to the data collected from the meteorological stations of the state forest department for 1980–2010, the mean annual rainfall ranges from 865 to 1196 mm (Chaturvedi et al. 2011a). About 85% of the annual rainfall occurs during the monsoon (rainy) season from the south-west monsoon, and the remaining from the few showers in December and in May–June. There is an extended dry period of about 9 months (October–mid June) in the annual cycle (Jha & Singh 1990). The monthly rainfall varies from 6 mm in April to 334 mm in August (Chaturvedi et al. 2012b). Soils of the study area are residual, ultisols, sandy-loam in texture, reddish to dark gray in colour and extremely poor in nutrients (Chaturvedi & Raghubanshi 2011). Recently estimated physico-chemical properties of soils of the study region have been described in Chaturvedi & Raghubanshi (2015b). The forest region exhibit patchiness in the species composition due to small variations in the environmental variables (Chaturvedi et al. 2011b). Species composition, distribution and diversity (Chaturvedi & Raghubanshi 2014, Chaturvedi et al. 2017b), and seasonal growth (Chaturvedi et al. 2011c, 2013, 2014) of woody species is highly influenced by soil moisture content. The density-DBH distributions in the forest region exhibited low DBH-biased structure, where the average density of seedlings, saplings and adults were 9,261±1,511, 799±154 and 297±42, respectively (Chaturvedi & Raghubanshi 2014).

Leaf area index (LAI) estimation

The data was collected from the private teak plantation in the forest region of Vindhyan Highlands. The field sampling was done in September, when teak trees were fully-leaved. We selected ten teak trees in each of the ten stem diameter (D, cm) classes (viz. ≥ 3.2 to < 6.4; ≥ 6.4 to < 9.6; ≥ 9.6 to < 12.7; ≥ 12.7 to < 15.9; ≥ 15.9 to < 19.1; ≥ 19.1 to < 22.3; ≥ 22.3 to < 25.5; ≥ 25.5 to < 28.7; ≥ 28.7 to < 31.8; ≥ 31.8). For the individuals < 3 m height, D was measured below the lowest branch and away from stem irregularities, and for others having ≥ 3 m height, D was measured at 1.37 m above ground. Projected crown area for each selected individual was estimated by the line-intercept method, which is expected to provide most accurate canopy cover estimate (Fiala et al. 2006). In this method, horizontal distances covered by the live crown was recorded along a line transect radiating out from the main stem for each tree, in 6–8 directions depending upon the crown irregularities. For each tree, along with each transect line, the distance of the first point of interception of the crown to the last point of interception was recorded (to the nearest dm), with the help of a clinometer to verify the interception of the crown directly overhead. After canopy cover estimation, all selected individuals were harvested, and their height (H) and D were recorded. The foliage of trees having < 9.6 cm D was separated and dry biomass of leaves for each individual tree was estimated by drying in an oven at 80 °C to constant weight. For the trees having ≥ 9.6 cm D, it was impractical to pick off all leaves of the large tree, therefore, initially, twigs with leaves were cut and weighed in bulk for each tree separately on a hanging scale (0.1 kg precision, 200 kg capacity). Around 10 to 20% of the bulk was defoliated (foliage was sampled proportionally to the position of foliage along the branch) and leaves and twigs were weighed separately to calculate the leaf-to-twig mass fraction for that tree. This fraction was used to detect the foliage green weight for each individual tree. The defoliated leaves were dried at 80 °C to constant weight, separately for each tree to know the moisture content in the leaves. By subtracting the moisture content from the foliage green weight, foliage dry weight for each individual tree was calculated. Before drying, 50 leaves were randomly taken from each individual tree for the estimation of specific leaf area (SLA) following Cornelissen et al. (2003). After SLA estimation, the dry weight of the leaves was pooled with the foliage dry weight of the tree from where the leaves were taken. Wood samples for the estimation of p were collected by using a stem borer (Turner & Cole 1973). After removing the bark, wood core was taken from each sapling at the height where D was measured and the samples were sealed in polythene bags and were taken to the laboratory. Volumes of fresh wood samples were measured by water displacement method and the samples were dried in a well-ventilated oven at 101–105 °C till constant weight (Williamson & Wiemann 2010). The values were expressed as g.cm⁻³.

Statistical analysis

To estimate the one-sided leaf tissue area for each tree, their foliage dry weights were multiplied with their SLA. Thus, we determined LAI of each tree by harvest method as the ratio of total one-sided leaf area and the canopy cover. Standard deviation, skewness and kurtosis of the LAI of each D-class were calculated with the help of Microsoft Excel 2007. Data of all the ten D-classes were used to develop regression models for the
estimation of LAI on the basis of ρ, D and H. The regression models used for the prediction of LAI were of the form, linear, logistic, Gompertz and Chapman. The best model for each D-class was selected by assessing the goodness of fit based on the coefficients of determination, standard errors of the estimate, P values, and average deviation (%) from the observed data. We applied t test for comparison of LAI estimated by harvest method and that by the regression model. Similarly, we developed regression models for the estimation of LAI for all the ten D-classes, and selected most appropriate models. All the statistical analyses were done using SPSS (ver. 16) package. To check for the strength of the relationship between LAI estimated by the two methods, we regressed the harvest data of each D-class against the estimates obtained through the newly developed model by using SigmaPlot (ver.11).

RESULTS

Table 1. Range of wood specific gravity (ρ), stem diameter (D), height (H), specific leaf area (SLA) and canopy cover (CC) in the 10 stem diameter classes of teak.

<table>
<thead>
<tr>
<th>S.No.</th>
<th>D-class (cm)</th>
<th>ρ (g.cm⁻³)</th>
<th>D (cm)</th>
<th>H (m)</th>
<th>SLA(cm².g⁻¹)</th>
<th>CC (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>≥ 3.2 – &lt; 6.4</td>
<td>0.523-0.592</td>
<td>3.25-6.15</td>
<td>3.8-8.2</td>
<td>70.1-73.2</td>
<td>0.95-1.77</td>
</tr>
<tr>
<td>2.</td>
<td>≥ 6.4 – &lt; 9.6</td>
<td>0.611-0.647</td>
<td>6.50-9.36</td>
<td>8.4-11.9</td>
<td>68.4-70.6</td>
<td>2.01-3.80</td>
</tr>
<tr>
<td>3.</td>
<td>≥ 9.6 – &lt; 12.7</td>
<td>0.639-0.661</td>
<td>9.83-12.6</td>
<td>12.3-15.2</td>
<td>67.3-70.2</td>
<td>2.83-6.60</td>
</tr>
<tr>
<td>4.</td>
<td>≥ 12.7 – &lt; 15.9</td>
<td>0.654-0.693</td>
<td>13.2-15.5</td>
<td>15.4-17.8</td>
<td>66.2-69.1</td>
<td>4.91-10.2</td>
</tr>
<tr>
<td>5.</td>
<td>≥ 15.9 – &lt; 19.1</td>
<td>0.688-0.726</td>
<td>16.2-18.6</td>
<td>17.8-19.8</td>
<td>65.2-67.9</td>
<td>10.2-13.2</td>
</tr>
<tr>
<td>6.</td>
<td>≥ 19.1 – &lt; 22.3</td>
<td>0.718-0.747</td>
<td>19.4-22.1</td>
<td>19.1-21.2</td>
<td>64.3-67.8</td>
<td>11.3-16.6</td>
</tr>
<tr>
<td>7.</td>
<td>≥ 22.3 – &lt; 25.5</td>
<td>0.735-0.749</td>
<td>22.6-25.4</td>
<td>20.4-23.3</td>
<td>63.8-66.8</td>
<td>15.9-27.3</td>
</tr>
<tr>
<td>8.</td>
<td>≥ 25.5 – &lt; 28.7</td>
<td>0.726-0.755</td>
<td>25.6-28.5</td>
<td>22.8-25.8</td>
<td>62.9-65.8</td>
<td>26.4-30.2</td>
</tr>
<tr>
<td>9.</td>
<td>≥ 28.7 – &lt; 31.8</td>
<td>0.751-0.768</td>
<td>28.9-31.6</td>
<td>24.3-26.4</td>
<td>61.9-64.6</td>
<td>31.2-39.6</td>
</tr>
<tr>
<td>10.</td>
<td>≥ 31.8</td>
<td>0.769-0.774</td>
<td>32.0-39.8</td>
<td>24.8-33.3</td>
<td>60.4-62.8</td>
<td>39.6-44.2</td>
</tr>
</tbody>
</table>

Figure 1. Relationships between the log transformed values of ρD² and the log transformed values of LAI estimated by harvest method for teak trees. For regression models, see Table 2. ρ, wood specific gravity (g cm⁻³); D, stem diameter (cm); H, height (m). n = 100.
Table 2. Regression models [linear, \( Y = Y_0 + aX \); logistic, \( Y = Y_0 + \frac{a}{1 + \left(\frac{X}{X_0}\right)^b} \); Gompertz, \( Y = Y_0 + ae^{-e^{(X-x_0)/b}} \); Chapman, \( Y = Y_0 + a(1-e^{-bx})^c \)] for estimating leaf area index (LAI) of teak. \( \rho \), wood specific gravity (g cm\(^{-3}\)); D, stem diameter at breast height (cm); H, tree height (m).

<table>
<thead>
<tr>
<th>S.No.</th>
<th>Model</th>
<th>( R^2 ) value</th>
<th>Standard error of estimate</th>
<th>Average deviation (%)</th>
<th>( P ) value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>( \ln(LAI) = 0.796 + 0.105\ln(D^2) )</td>
<td>0.381</td>
<td>0.167</td>
<td>4.708</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2.</td>
<td>( \ln(LAI) = 1.225 + \frac{0.474}{1 + \left(\frac{\ln(D^2)}{6.327}\right)^{-2.148}} )</td>
<td>0.685</td>
<td>0.115</td>
<td>4.018</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>3.</td>
<td>( \ln(LAI) = 1.224 + 0.552e^{-e^{\left(\frac{\ln(D^2)-6.212}{0.346}\right)}} )</td>
<td>0.651</td>
<td>0.126</td>
<td>4.165</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>4.</td>
<td>( \ln(LAI) = 6.407 + 0.552(1 - e^{-1.705+\ln(D^2)})^{39874.7} )</td>
<td>0.643</td>
<td>0.139</td>
<td>4.193</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>5.</td>
<td>( \ln(LAI) = 0.859 + 0.098\ln(D^2) )</td>
<td>0.399</td>
<td>0.158</td>
<td>4.518</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>6.</td>
<td>( \ln(LAI) = 1.225 + \frac{0.478}{1 + \left(\frac{\ln(D^2)}{6.157}\right)^{-19.51}} )</td>
<td>0.708</td>
<td>0.103</td>
<td>3.592</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>7.</td>
<td>( \ln(LAI) = 1.224 + 0.557e^{-e^{\left(\frac{\ln(D^2)-6.032}{0.629}\right)}} )</td>
<td>0.670</td>
<td>0.124</td>
<td>4.036</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>8.</td>
<td>( \ln(LAI) = 6.397 + 0.557(1 - e^{-1.594+\ln(D^2)})^{15128.4} )</td>
<td>0.651</td>
<td>0.132</td>
<td>4.101</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>9.</td>
<td>( \ln(LAI) = 0.441 + 0.072\ln(D^2)H )</td>
<td>0.353</td>
<td>0.171</td>
<td>4.945</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>10.</td>
<td>( \ln(LAI) = 1.224 + \frac{0.467}{1 + \left(\frac{\ln(D^2)H}{14.00}\right)^{-37.96}} )</td>
<td>0.672</td>
<td>0.116</td>
<td>4.057</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>11.</td>
<td>( \ln(LAI) = 1.223 + 0.530e^{-e^{\left(\frac{\ln(D^2)H-13.83}{0.74}\right)}} )</td>
<td>0.645</td>
<td>0.127</td>
<td>4.168</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>12.</td>
<td>( \ln(LAI) = 1.221 + 0.566(1 - e^{-1.247+\ln(D^2)H})^{32760000.0} )</td>
<td>0.644</td>
<td>0.136</td>
<td>4.248</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>13.</td>
<td>( \ln(LAI) = 0.503 + 0.069\ln(D^2)H )</td>
<td>0.361</td>
<td>0.169</td>
<td>4.825</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>14.</td>
<td>( \ln(LAI) = 1.224 + \frac{0.469}{1 + \left(\frac{\ln(D^2)H}{13.83}\right)^{-35.67}} )</td>
<td>0.678</td>
<td>0.119</td>
<td>4.016</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>15.</td>
<td>( \ln(LAI) = 1.223 + 0.534e^{-e^{\left(\frac{\ln(D^2)H-13.66}{0.747}\right)}} )</td>
<td>0.646</td>
<td>0.127</td>
<td>4.166</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>16.</td>
<td>( \ln(LAI) = 6.479 + 0.548(1 - e^{-1.271+\ln(D^2)H})^{34981495.2} )</td>
<td>0.647</td>
<td>0.132</td>
<td>4.232</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

For all the ten D-classes, ranges of \( \rho \), D, H, SLA and canopy cover (CC) are shown in table 1. Descriptive statistics (i.e., maximum and minimum values, mean, standard deviation, skewness and kurtosis) of the datasets of LAI are shown in Appendix I. For the estimation of LAI, the developed regression models are reported in table 2. These models are constructed by combining all individuals in the ten D-classes (n = 100). The difference of variability explained between the worst and the best model was 36% (Table 2). We observed more than 60% variability in the LAI, explained by non-linear regression models. The models including \( \rho \) and D had greater \( R^2 \), and lower standard error of estimate and average deviation. Among the four types of regression models developed for predicting LAI, greater \( R^2 \), and lower standard error of estimate and average deviation were observed for the logistic model (Table 2). For the estimation of LAI, irrespective of the effect of stem diameter, we selected model 6 from Table 2 (Fig. 1). The regression models for the estimation of LAI for all the ten D-classes are shown in Table 3. While developing these models, we could not get significant results (at 95%
level) for LAI for trees having stem diameter < 12.7 cm. For the D-classes having ≥ 12.7 cm stem diameter, Gompertz model produced most significant results (Table 3).

Table 3. Regression models for the 10 stem diameter (D, cm) classes of teak. Models are of the form, linear ($Y = Y_0 + aX$), and/or Gompertz ($Y = Y_0 + ae^{-(\frac{X}{b})}$), where, $Y$ = leaf area index, $X = pD^2$, $Y_0$, $a$ and $b$ are constants, $p$ = wood specific gravity (g cm$^{-3}$). $n$ = 10. Here, only linear regression models and most significant non-linear models are shown.

<table>
<thead>
<tr>
<th>Model No.</th>
<th>D-class (cm)</th>
<th>Model</th>
<th>$R^2$ value</th>
<th>Standard error of estimate</th>
<th>Average deviation (%)</th>
<th>$P$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>≥ 3.2 to &lt; 6.4</td>
<td>$\ln Y = 1.252 + 0.026\ln X$</td>
<td>0.0031</td>
<td>0.212</td>
<td>0.148</td>
<td>&gt;0.050</td>
</tr>
<tr>
<td>2.</td>
<td>≥ 6.4 to &lt; 9.6</td>
<td>$\ln Y = 1.244 - 0.009\ln X$</td>
<td>0.0006</td>
<td>0.140</td>
<td>0.261</td>
<td>&gt;0.050</td>
</tr>
<tr>
<td>3.</td>
<td>≥ 9.6 to &lt; 12.7</td>
<td>$\ln Y = 1.235 - 0.016\ln X$</td>
<td>0.0002</td>
<td>0.229</td>
<td>0.357</td>
<td>&gt;0.050</td>
</tr>
<tr>
<td>4.</td>
<td>≥ 12.7 to &lt; 15.9</td>
<td>$\ln Y = -3.968 + 1.029\ln X$</td>
<td>0.6067</td>
<td>0.100</td>
<td>1.368</td>
<td>&lt;0.010</td>
</tr>
<tr>
<td>5.</td>
<td>≥ 15.9 to &lt; 19.1</td>
<td>$\ln Y = 1.023 + 0.287e^{-(\frac{\ln X - 4.937}{0.092})}$</td>
<td>0.8579</td>
<td>0.069</td>
<td>0.792</td>
<td>&lt;0.010</td>
</tr>
<tr>
<td>6.</td>
<td>≥ 19.1 to &lt; 22.3</td>
<td>$\ln Y = -3.583 + 0.891\ln X$</td>
<td>0.6448</td>
<td>0.068</td>
<td>1.178</td>
<td>&lt;0.010</td>
</tr>
<tr>
<td>7.</td>
<td>≥ 22.3 to &lt; 25.5</td>
<td>$\ln Y = -3.193 + 0.779\ln X$</td>
<td>0.4826</td>
<td>0.077</td>
<td>1.582</td>
<td>&lt;0.050</td>
</tr>
<tr>
<td>8.</td>
<td>≥ 25.5 to &lt; 28.7</td>
<td>$\ln Y = -6.156 + 1.226\ln X$</td>
<td>0.8449</td>
<td>0.046</td>
<td>0.937</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>9.</td>
<td>≥ 28.7 to &lt; 31.8</td>
<td>$\ln Y = -2.023 + 0.561\ln X$</td>
<td>0.5996</td>
<td>0.040</td>
<td>1.026</td>
<td>&lt;0.010</td>
</tr>
<tr>
<td>10.</td>
<td>≥ 31.8</td>
<td>$\ln Y = 1.553 + 0.091e^{-(\frac{\ln X - 7.590}{0.002})}$</td>
<td>0.6719</td>
<td>0.039</td>
<td>0.728</td>
<td>&lt;0.010</td>
</tr>
</tbody>
</table>

Figure 2. Average LAI (±1 S.E.) across the 10 diameter classes of teak estimated by the two methods.

Harvested LAI exhibited strong relationships with the predicted values used in our models, especially in higher D-classes (Fig. 1). Average LAI for the ten D-classes estimated by harvest method and that from regression models are shown in figure 2. For the smallest D-class (i.e. ≥ 3.2 – < 6.4 cm), average LAI estimated by harvest method and allometric method were 3.2 and 3.1, respectively, and for the highest D-class (i.e. ≥ 31.8 cm), the average LAI estimated by harvest method and allometric method was almost same, i.e. 5.2. Statistically, the two estimates of LAI were different, only for the smaller three D-classes, i.e. ≥ 3.2 – < 6.4 cm ($t_{0.05} = 0.763$, $P = 0.049$), ≥ 6.4 – < 9.6 cm ($t_{0.05} = 0.857$, $P = 0.035$), and ≥ 9.6 – < 12.7 cm ($t_{0.05} = 0.716$, $P = 0.042$), whereas for other D-classes, the two estimates were not different (Fig. 2). The linear
regression models for LAI for all the ten D-classes were validated against the harvested LAI, and we observed significant results only for the higher seven D-classes (Fig. 3). Here we observed strong relationships for all the seven D-classes, with the greatest value of $R^2 = 0.85$ for the D-class, 22.3 to < 25.5 (Fig. 3).

![Graphs showing relationships between LAI and D-class for various stem diameters](image)

**Figure 3.** Relationships between the LAI of teak in the seven stem diameter (D) classes estimated by regression model (see Table 3) and by harvest method. [Note: For the lower three D-classes, the relationships were not significant]
DISCUSSION

We observed that the model containing wood specific gravity ($\rho$) as the estimator, better predicted LAI of teak tree. This exhibits that the $\rho$ is somehow linked with LAI. Tree canopy has a determining influence on wood quality, since the physiological processes originating in foliage regulate biological processes of wood formation (Larson 1969). Therefore, $\rho$ is also influenced by the tree canopy conditions. Wood specific gravity is also observed to be influenced by tree diameter, height and growth rate (Woodcock & Shier 2003). The range of $\rho$ observed in our study (0.52–0.77 g cm$^{-3}$) is comparable to the average values of $\rho$ (0.55–70 g cm$^{-3}$) found in Costa Rica (Pérez 2005) and other reportings for plantation grown teak (Bhat 1995, Brennan & Radomiljac 1998, Bhat 2000). We detected the logarithmic equation most appropriate for the estimation of LAI. According to Kerkhoff & Enquist (2009), several allometric characteristics of organisms are ‘multiplicative in nature’, therefore, allometric models constructed by log-transformed data is most acceptable.

Tree growth follows sigmoid/non-linear pattern (Zeide 1993) so linear regression models may not produce significant results for a wide range of explanatory variates. It has also been reported that the linear regression models become less effective as the number of explanatory variables and the complexity of data increases (De’ath & Fabricius 2001). When we attempted with linear as well as non-linear functions for the LAI estimations, for all D-classes combined together, we detected non-linear models as the better predictors of LAI estimates. Also, when we analysed the four models separately in the ten D-classes, the non-linear model (i.e. Gompertz) was more efficient compared to the linear model. The $R^2$ values of the non-linear models listed in Table 2 are quite good ($R^2 > 0.64$), and are very similar. We also observed the difference of < 7% variability explained between the worst and the best non-linear model. If the models including $\rho$ are compared with the models without $\rho$ but with the same variables (e.g. model 2 vs 6 and model 10 vs 14), we observed similar slope for the models including $\rho$ compared to the models without $\rho$. Moreover, on the basis of $R^2$, SEE and average deviation, all the non-linear models are very similar and equally good for the estimation of LAI.

Our allometric models predicted unsatisfactory LAI for trees with < 12.7 cm D (Table 3), however, the ability of allometric models for predicting LAI of large trees were stronger. According to Bailey & Harjanto (2005), teak trees at younger age (< 15 years) usually experience severe foliar damage due to cattle grazing and harvesting by humans. Cole & Ewel (2006) also emphasized the influence of weather, herbivores, and inter-plant competition on the foliage biomass. These might be the reasons for unpredictability in the estimation of LAI for trees with < 12.7 cm D. In a similar study, Cole & Ewel (2006) reported unsatisfactory prediction of leaf biomass by the allometric models applied for Cordia trees in 0–5 cm D-class. Similar to our observations, Cole & Ewel (2006) also observed stronger relations for larger trees with > 5 cm DBH.

Bréda (2003) compared the direct and indirect methods for LAI estimation and insisted that the underestimation of LAI by indirect methods could vary from 25% to 50% in forest stands. Due to canopy heterogeneity, calibration is necessary while estimating LAI through indirect methods (Bréda 2003). Therefore, for the estimation of LAI of teak we should choose the allometric equations which have fewer chances of error and estimates accurate value. Our allometric models are easy to apply and very practical, so it could be applied also at the locations outside where it is developed. Chave et al. (2004) also emphasized that the majority of systematic errors may result if the allometric models are applied for trees with greater D than those used to construct the allometry. The regression models developed in our study can be applied separately for the ten D-classes, and this could minimize the error occurring during non-destructive estimation of LAI of teak in different D-classes.

CONCLUSIONS

Previous studies have mostly adopted harvesting, litter trap methods and optical sensors for the estimation of LAI for teak stands. However, still there is scarcity of the method to determine LAI of individual teak tree. Moreover, the allometric models which are available are applied for a broad range of D-classes, due to the scarcity of models for a range of D-classes. Therefore, for accurate estimation of teak LAI, it is necessary to develop allometric models for different D-classes. Our study detected logistic models more appropriate for broad diameter range and Gompertz models for small D-classes. We observed that the linear models are not efficient in estimating teak LAI, compared to the non-linear models. Even among the three non-linear models, there is very less difference. Our allometric model could accurately estimate the spatial variability of teak LAI. Therefore, while choosing any appropriate technique, worker should keep in mind his own situation and the physiological process of interest.
ACKNOWLEDGEMENTS

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REFERENCES


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### Appendix I. Descriptive statistics of the leaf area index of teak used for developing regression models.

<table>
<thead>
<tr>
<th>Model No.</th>
<th>D-class (cm)</th>
<th>Min.-Max.</th>
<th>Mean</th>
<th>Standard deviation</th>
<th>Skewness</th>
<th>Kurtosis</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>≥ 3.2 – &lt; 6.4</td>
<td>2.642–4.975</td>
<td>3.807</td>
<td>0.749</td>
<td>0.168</td>
<td>-0.715</td>
</tr>
<tr>
<td>2.</td>
<td>≥ 6.4 – &lt; 9.6</td>
<td>2.610–3.873</td>
<td>3.382</td>
<td>0.434</td>
<td>-0.318</td>
<td>-0.938</td>
</tr>
<tr>
<td>3.</td>
<td>≥ 9.6 – &lt; 12.7</td>
<td>2.413–4.211</td>
<td>3.259</td>
<td>0.699</td>
<td>0.190</td>
<td>-1.503</td>
</tr>
<tr>
<td>4.</td>
<td>≥ 12.7 – &lt; 15.9</td>
<td>2.553–3.981</td>
<td>3.435</td>
<td>0.488</td>
<td>-0.753</td>
<td>-0.617</td>
</tr>
<tr>
<td>5.</td>
<td>≥ 15.9 – &lt; 19.1</td>
<td>2.905–4.165</td>
<td>3.593</td>
<td>0.380</td>
<td>-0.176</td>
<td>-0.221</td>
</tr>
<tr>
<td>6.</td>
<td>≥ 19.1 – &lt; 22.3</td>
<td>3.316–4.696</td>
<td>4.055</td>
<td>0.401</td>
<td>-0.275</td>
<td>0.043</td>
</tr>
<tr>
<td>7.</td>
<td>≥ 22.3 – &lt; 25.5</td>
<td>3.446–4.740</td>
<td>4.168</td>
<td>0.452</td>
<td>-0.365</td>
<td>-1.483</td>
</tr>
<tr>
<td>8.</td>
<td>≥ 25.5 – &lt; 28.7</td>
<td>4.515–5.396</td>
<td>4.897</td>
<td>0.293</td>
<td>0.436</td>
<td>-0.976</td>
</tr>
<tr>
<td>9.</td>
<td>≥ 28.7 – &lt; 31.8</td>
<td>4.769–5.258</td>
<td>5.053</td>
<td>0.143</td>
<td>-0.757</td>
<td>0.512</td>
</tr>
<tr>
<td>10.</td>
<td>≥ 31.8</td>
<td>4.960–5.590</td>
<td>5.224</td>
<td>0.207</td>
<td>0.384</td>
<td>-0.860</td>
</tr>
</tbody>
</table>

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